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Vulnérabilité des écosystèmes montagnards aux changements globaux par une modélisation spatialement explicite - implications pour la conservation -

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A mon père, Jo

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Erreur : mémoire épuisée (limite atteinte ?)
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Le texte qui suit est composé d'une introduction, de cinq chapitres et d'une synthèse. L'introduction et la synthèse sont rédigées en français. Les chapitres sont écrits en anglais et constituent des articles publiés (chapitres I et II), soumis (chapitre III) ou en préparation (chapitres IV et V) dont je suis premier auteur. Tous ces articles ont été réalisés en étroite collaboration avec mes encadrants (Wilfried Thuiller et Sébastien Lavergne), avec Damien Georges, ingénieur programmeur, d'autres chercheurs du LECA (Sandra Lavorel et Rolland Douzet) et d'autres laboratoires (Dominique Gravel et Pascal Vittoz), des botanistes du CBNA (Luc Garraud, Jérémie Van Es et Sylvain Abdulhak) et avec le Parc national des Ecrins (Cédric Dentant et Richard Bonet). Les travaux dont je suis co-auteur sont présentés en annexe.

Liste des contributions

Chapitres

Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L. Thuiller, W. (2012) Niche breadth, rarity and ecological characteristics within a regional flora spreading over large environmental gradients. *Journal of Biogeography*, **39**, 204-214.

Boulangeat, I., Gravel, D. and Thuiller, W. (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters,* **15**, 584-593.

Boulangeat, I., Philippe, P., Abdulhak, S., Douzet, R., Garraud, L., Lavergne Sébastien, Lavorel S., Van Es, J., Vittoz, P., and Thuiller, W. Optimizing plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. *Accepted in Global Change Biology.*

Boulangeat, I., Georges, D., Dentant, C., Thuiller, W. FATE-H: A spatially and temporally explicit hybrid model for predicting the vegetation structure and diversity at regional scale. *In preparation.*

Boulangeat, I., Georges, D., Dentant, C., Bonet, R., Van Es, J., Abdulayak, A., Zimmermann, N.E. and Thuiller, W. Consequences of climate and land use change on the vegetation structure and diversity in the Ecrins National Park. *In preparation*.

Annexes

Gallien, L., Münkemüller, T., Albert, C.H., **Boulangeat, I.** & Thuiller, W. (2010) Predicting species invasions: where to go from here? *Diversity and Distributions*, **16**, 331-342.

Thuiller W., Gallien, L., **Boulangeat, I.,** de Bello, F., Münkemüller, T., Roquet-Ruiz, C. & Lavergne, S. (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions*, **16**, 461-475.

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Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., **Boulangeat, I.,** Hodgson, J.A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V.M., Bullock, J.M. Dispersal and biodiversity responses to climate change. *Submitted.*

Meynard, C.H., Lavergne, S., **Boulangeat, I.,** Garraud, L., Van Es, J., Mouquet, N., Thuiller, W. Disentangling the drivers of metacommunity structure across spatial scales. *Submitted*.

TABLE DES MATIÈRES

INTRODUCTION

L'EROSION DE LA BIODIVERSITE FACE AUX CHANGEMENTS ENVIRONNEMENTAUX

QU'EST CE QUE LA BIODIVERSITE ?

C'est à Rio en 1992, dans le cadre d'un sommet planétaire sur l'environnement et le développement, que le terme « *biodiversité* » est apparu pour la première fois, forme contractée de « *diversité biologique* ». Le concept sous-jacent est plutôt né dans le milieu politique autour des années 1980 et reste aujourd'hui très mal défini scientifiquement. Dès le début, il est utilisé tantôt comme synonyme de la richesse en espèces, tantôt décrivant plus largement toute sorte de vie sur Terre (Hamilton 2005). Pendant des années, il est utilisé par la communauté scientifique, principalement parce que sa popularité permet d'attirer les financeurs sur des travaux de recherche plutôt théoriques, dont l'intérêt est souvent difficile à démontrer à court terme (Hamilton 2005a). Cette utilisation très diverse du terme *biodiversité* conduit DeLong (DeLong 1996) à relever 85 définitions différentes, soulignant le flou qui règne autour de ce terme. En 2003, la convention internationale sur la biodiversité (CBD) utilise une très large définition, qui inclue trois niveaux d'organisation : les gènes, les espèces et les écosystèmes. Cette définition fait référence à tout ce qui crée et maintient la diversité des espèces, notamment la variété des gènes, les réseaux trophiques et les interactions des espèces entre elles et avec leur environnement physique. Nous considérons dans cette thèse plus particulièrement la diversité écologique, qui comprend la diversité des espèces, des ressources et des habitats (Hamilton 2005a).

LES CHANGEMENTS ENVIRONNEMENTAUX ET LA CRISE DE LA BIODIVERSITE

Un point de rupture : la révolution industrielle

Au cours du XIXe siècle, les sociétés agraires et artisanales achèvent de se transformer en sociétés de commerce et d'industrie. Cette révolution industrielle se traduit par une considérable intensification de la pression de l'Homme sur les écosystèmes, comme l'augmentation de l'utilisation

des énergies fossiles et une déforestation massive ou encore l'émergence de pollutions diverses. La croissance démographique qui l'a accompagnée a entrainé un accroissement de la demande de produits agricoles, ayant pour conséquence une profonde transformation de l'agriculture. En plaine, celle-ci va s'intensifier et les sols vont être surexploités. Au contraire, en zone de montagne l'exode rural va conduire à une déprise agricole et au développement des zones urbaines. Ces changements dans les pratiques agricoles et l'utilisation des terres sont la première cause des changements environnementaux au niveau mondial.

Cette époque est également considérée comme un point de rupture après lequel le niveau de CO2 dans l'atmosphère a fortement et rapidement augmenté, entrainant un changement climatique brutal et inquiétant les sociétés. L'augmentation de la température moyenne à la surface du globe n'est aujourd'hui plus mise en doute (Fig. i.1) et ce réchauffement a clairement été induit par l'activité humaine de l'ère industrielle (Vitousek *et al.* 1997). Il est déjà observé au niveau du globe mais aussi localement, par exemple dans les zones de montagne (Fig. i.1b). Les prévisions des climatologues pour les 100 ans à venir suivent la même tendance, avec une probable accélération (IPCC 2007b). Le réchauffement global serait de l'ordre de 1,4 °C à 5,8 °C, associé à une augmentation de la fréquence des évènements extrêmes (ex. sècheresse) et à une modification des régimes de précipitations (IPCC 2007b).

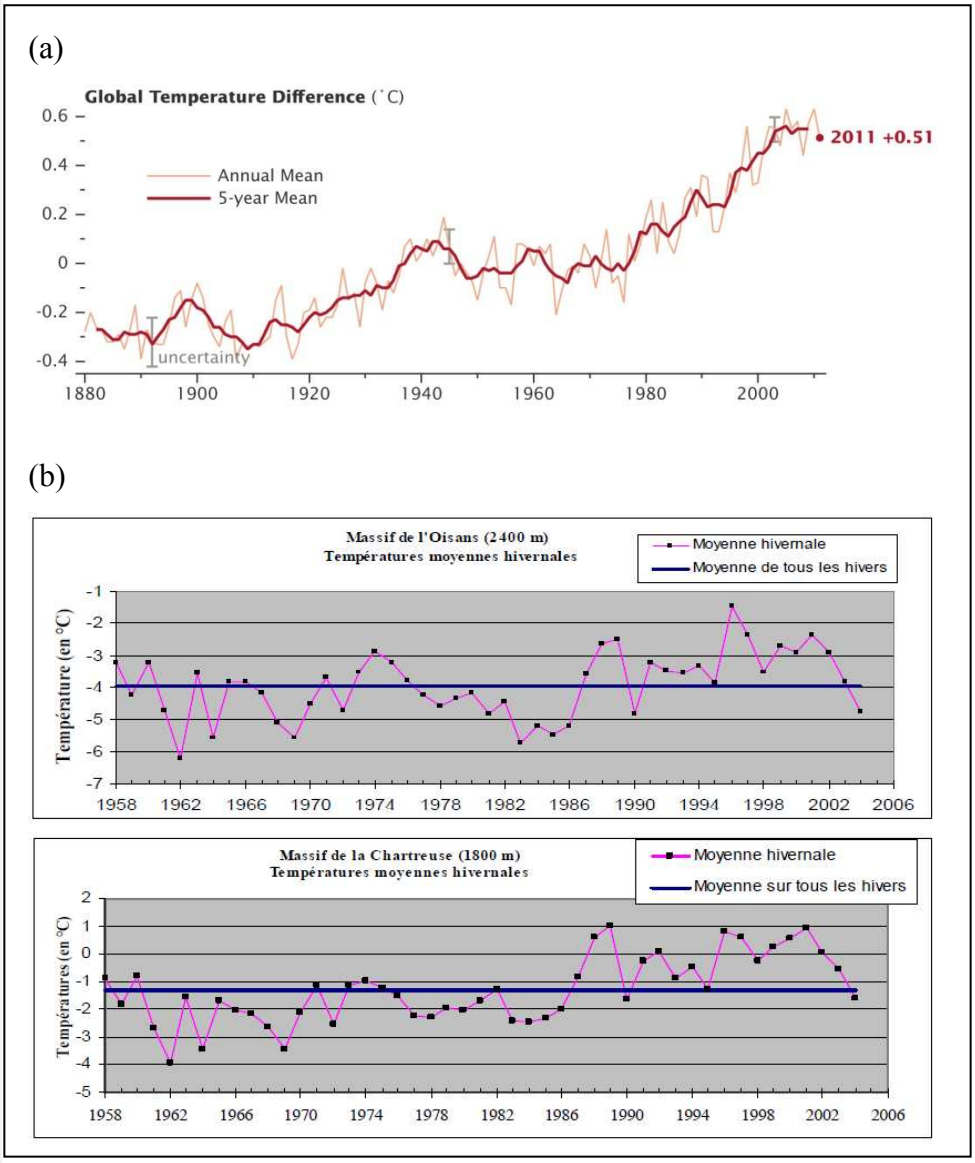

Fig. i.1. Augmentation des températures à différentes échelles (a) Augmentation de la température à l'échelle du globe. Les températures moyennes fluctuent énormément d'une année sur l'autre, c'est pourquoi les scientifiques se focalisent sur les tendances décennales. Depuis 1980, 90% des années les plus chaudes se trouvent après l'an 2000. Comme les gaz à effet de serre et le CO2 atmosphérique continuent d'augmenter, on s'attend à ce que les tendances restent à l'augmentation. (Source: NASA Goddard Institute for Space Studies. Image: NASA Earth Observatory, Robert Simmon). **(b)** Evolution des températures hivernales moyennes dans les Alpes françaises, sur deux massifs. Les températures sont assez variables selon les années mais sont sensiblement plus chaudes dans la dernière décade. Cet effet est moins significatif à plus haute altitude (Source : Navarre 2007/PGRN).

Conséquences pour la biodiversité et les écosystèmes

D'une manière générale, tous les composants de la biodiversité, des organismes aux biomes, peuvent être affectés par le changement climatique (Parmesan 2006) et par les changements relatifs à l'utilisation des terres (Vitousek *et al.* 1997). En termes d'espèces, des extinctions à un taux jamais atteint sont attendues (Millennium Ecosystem Assessment 2005a; Pereira *et al.* 2010), certaines pouvant entrainer des cascades d'extinctions dues aux relations biotiques entre espèces (Koh *et al.* 2004; Memmott *et al.* 2007; Rafferty & Ives 2011). Par exemple, les changements climatiques peuvent causer des décalages phénologiques entre des plantes et leurs pollinisateurs, conduisant à des extinctions potentielles dans les deux groupes à la fois (Harrington *et al.* 1999). En termes d'habitats, on a aussi observé d'importantes

modifications dues aux changements environnementaux. Par exemple dans les Alpes, la déprise agricole, et plus particulièrement l'abandon des pâturages en limite forestière, a engendré une remontée de la limite supérieure altitudinale des arbres (Fig. i.2 et Gehrig-Fasel *et al.* 2007).

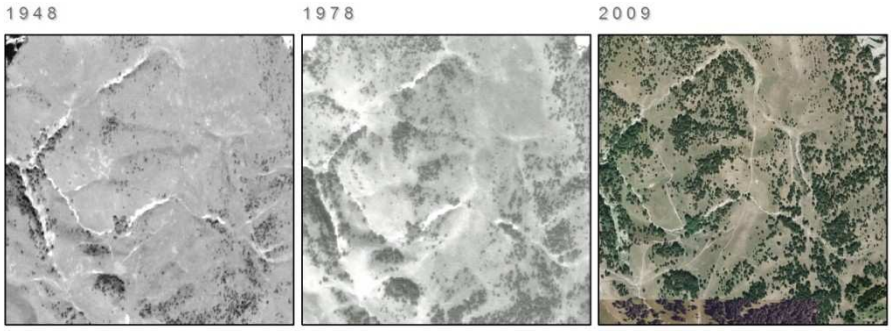

Fig. i.2 Evolution de la limite forestière dans la Réserve Naturelle des Hauts Plateaux du Vercors. Ces photos aériennes ont été prises dans les Alpes à plus d'un demi-siècle d'écart. Elles illustrent la recolonisation des arbres due à l'abandon des pâturages. Source : projet Biodiversa CAMELEON (Julien Renaud).

Encore peu d'études ont cherché à prédire la dynamique des paysages à l'échelle régionale, en prenant en compte les effets combinés des changements climatique et d'utilisation des terres sur l'évolution de la répartition de la végétation. Un des grands enjeux de la communauté scientifique est de combler ce manque par la collecte de nouvelles données, de nouvelles connaissances et le développement de nouveaux modèles. Ma thèse se place exactement dans ce cadre et propose des développements méthodologiques (chapitre III) pour permettre à un nouveau modèle dynamique de la biodiversité (chapitre IV) d'explorer ces questions (chapitre V).

Prédire le futur de la biodiversité, une demande sociétale

Si la biodiversité fait aujourd'hui partie des enjeux politiques, c'est parce qu'on lui reconnait une importance vitale. La diversité des espèces dans une communauté permettrait sa stabilité (Frank & McNaughton 1991) et sa résistance aux invasions (Naeem *et al.* 2000), ainsi qu'une meilleure productivité (Waide *et al.* 1999; Hooper *et al.* 2005), l'ensemble permettant à l'écosystème de fournir des services indispensables à la vie humaine. Ces services écosystémiques, qui sont les bénéfices que les humains tirent des écosystèmes (Millennium Ecosystem Assessment 2005), comprennent par exemple les ressources naturelles (eau, nourriture et matières premières), la régulation du

climat et des ravageurs, la séquestration du carbone ou la pollinisation par les insectes. Ce sont ces bénéfices qui sont menacés par la crise de la biodiversité.

Afin d'améliorer la préservation des systèmes naturels face aux changements globaux, plusieurs institutions internationales ont vu le jour. En 1988, le GIEC (Groupement intergouvernemental d'experts sur l'évolution du climat) a été créé pour synthétiser les connaissances scientifiques mondiales sur le climat. Cet organisme a joué un rôle essentiel dans la prise de conscience des changements globaux. Aujourd'hui, deux autres organismes existent, plus particulièrement axés sur la préservation de la biodiversité. La Convention sur la diversité biologique (CDB) est l'organe qui encadre les négociations internationales visant à enrayer la perte de biodiversité et des services qui y sont associés, et la Plateforme sur la biodiversité et les services écosystémiques (IPBES), nouvellement crée, regroupera les données scientifiques et produira des recommandations sur la base des travaux des chercheurs du monde entier. La recherche que j'ai menée lors de ma thèse a particulièrement été stimulée par cette demande sociétale. Pour mieux comprendre l'émergence, la maintenance et le déclin de la biodiversité, de nouveaux modèles sont nécessaires. Ils doivent néanmoins se baser sur un cadre théorique consistent afin de produire des scenarios robustes. La section suivante est destinée à présenter ce cadre conceptuel.

CADRE CONCEPTUEL

LA COEXISTENCE DES ESPECES

Le concept de niche et la spécialisation écologique

Comprendre les mécanismes qui créent et maintiennent la diversité des espèces est crucial pour prévoir l'influence des changements environnementaux. Dans ce domaine, les théories de la coexistence des espèces jouent un rôle central. La principale, développée au 20ème siècle, est basée sur le concept de niche écologique, décrite de multiples façons par Grinnell (1917), Elton (1927), Hutchinson (1957), ou encore Levins et MacArthur (1966). Dans tous les cas, la notion de ressources est centrale (Chase & Leibold 2003). La niche est généralement définie comme les conditions nécessaires à la survie de l'espèce (ex. type de ressources) et l'impact qu'elle a sur les ressources (ex. exploitation des ressources). La différenciation de niche permet à chaque espèce de se distinguer par son rôle ou ses besoins et d'éviter ainsi la compétition, ce qui aboutit à une coexistence stable des espèces. Ce mécanisme de coexistence est un effet « *stabilisateur* » (Chesson 2000a). A l'inverse, deux espèces ayant des niches trop semblables vont entrer en compétition jusqu'à ce que l'une soit exclue (principe de Gause, 1934). Cependant, si les deux espèces sont suffisamment similaires, elles vont coexister temporairement de la même manière que deux individus d'une même espèce. La coexistence est alors le résultat d'un d'effet « *égalisateur* » (Chesson 2000a).

Le long d'un gradient environnemental considéré, deux types de différenciation de niches peuvent être distingués, selon deux paramètres principaux : la position et la largeur (Fig. i.3). Ces deux paramètres caractérisent deux types de spécialisation à l'origine de la coexistence de nombreuses espèces (Evans *et al.* 2005; Mason *et al.* 2008). La spécialisation de position, appelée « *marginalité* », a lieu quand la niche d'une espèce est positionnée là où les conditions environnementales sont marginales et rares (ex. extrémité du gradient). La spécialisation écologique fait plus souvent référence à l'amplitude du gradient sur

laquelle s'étend la niche de l'espèce (Futuyma & Moreno 1988). Cette spécialisation, appelée aussi « *largeur de niche* » est illustrée Fig. i.3 (à droite, espèce 1).

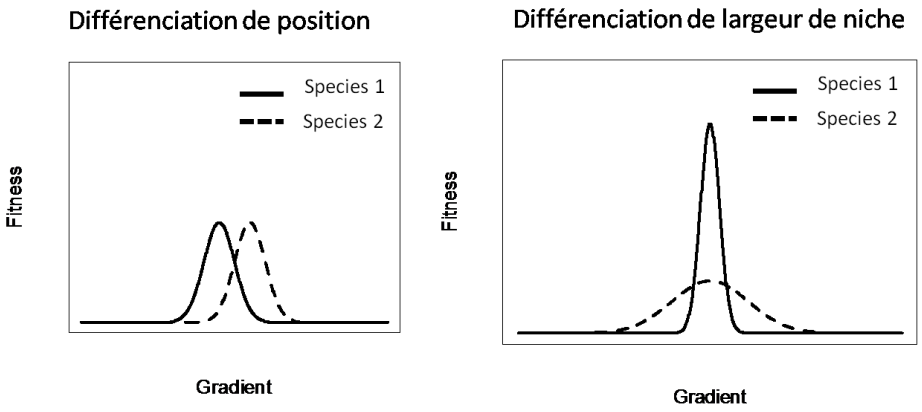

Fig. i.3. Différenciation de niche. A gauche, selon la position, à droite, selon la tolérance. La fitness détermine la compétitivité de l'espèce. Les deux espèces se partagent les zones du gradient pour lesquelles elles sont meilleures compétitrices. Dans les deux cas, les fitness sont différentes en tout point du gradient, sauf au croisement des courbes ou la relation entre les espèces est neutre.

La spécialisation, fondamentale pour la coexistence des espèces et le maintien d'une forte diversité, est très importante pour établir la vulnérabilité des espèces. Par exemple, en cas de modification rapide des facteurs environnementaux, les espèces ayant une largeur de niche restreinte peuvent être plus affectées que les plus généralistes, si la direction du changement les exposent fortement (McKinney 1997; Clavel *et al.* 2011).

Beaucoup d'études sur la spécialisation ont ciblé des petits groupes d'espèces dans leur région. Au contraire, encore peu d'études ont cherché à décrire et expliquer les différents degrés de spécialisation d'une flore complète sur une région biogéographique hétérogène. D'autre part, la majorité des études se sont focalisées sur quelques axes de différenciation de niche sélectionnés a priori. Prendre en compte de nombreux axes de différenciation de niche et relier le degré de spécialisation à différents critères de rareté ainsi qu'à des traits d'histoire de vie devrait pourtant pouvoir permettre de mieux comprendre les mécanismes de distribution et de coexistence des espèces et estimer leur vulnérabilité (voir Chapitre I)

Distinction entre facteurs biotiques et abiotique : Elton vs Grinnell

La niche écologique peut être définie selon deux grandes perspectives. La niche 'grinnellienne' est définie par les besoins d'une espèce pour sa survie (Grinnell 1917) et elle est délimitée par des facteurs abiotiques (conditions climatiques, ressources disponibles…). La niche 'eltonienne' fait référence à l'impact ou le rôle fonctionnel d'une espèce dans une communauté (Elton 1927). Elle est déterminée au travers des interactions biotiques (compétition, facilitation…). Deux espèces ayant des niches grinnelliennes semblables (besoins physiologiques similaires) peuvent donc coexister si elles se différencient sur le plan eltonien (Chase & Leibold 2003).

En ce qui concerne la spécialisation écologique, la largeur de niche grinnellienne sera souvent mesurée par la tolérance aux facteurs bioclimatiques (Devictor *et al.* 2010), tandis que la largeur de niche eltonienne pourra par exemple être évaluée par le nombre d'hôtes, de pollinisateurs, de proies (Devictor *et al.* 2010) ou plus généralement par la variation (intra-spécifique) de traits fonctionnels impliqués dans les interactions biotiques. D'autres mesures telles que celle proposée par Fridley (2007), ne distinguent pas les différents axes de niche mais tentent d'en prendre en compte une multitude. En effet, Fridley (2007) propose d'inférer l'amplitude écologique des espèces à partir de leurs patrons de cooccurrences dans les communautés. Une espèce dont les voisines changent d'une communauté à l'autre sera considérée comme généraliste. A l'inverse, une espèce dont le taux de changement de ces co-occurrentes varie peu sera considérée comme ayant une niche écologique restreinte. Cette approche nécessite peu de données, puisque qu'il n'est pas nécessaire de choisir a priori les axes de niche importants pour chaque espèce. Elle permet donc l'analyse de grands jeux de données et peut mettre en évidence la relation générale entre la spécialisation et d'autres mesures de la rareté ou avec les stratégies écologiques des espèces (voir Chapitre I)

La dimension spatio-temporelle et la théorie neutre de la biodiversité

La théorie de la niche a suscité de nombreuses critiques, notamment parce qu'elle ne permettait pas d'expliquer le fonctionnement des écosystèmes où le nombre d'espèces est supérieur au type/nombre de ressources et aux moyens de les exploiter (Bell 2001; Hubbell 2001). Ces écosystèmes riches en espèces comme les forêts tropicales ou les barrières de corail (Chave 2004) ont inspiré la théorie neutre de la biodiversité « *The Unified Neutral Theory of Biodiversity and Biogeography* » (Hubbell 2001). Ce modèle théorique, basé sur des individus, met en jeu des processus stochastiques (survie, dispersion, spéciation), et permet d'expliquer la richesse en espèces des communautés naturelles (Hubbell 2001). Le modèle neutre est un équilibre stochastique entre la spéciation et l'extinction des espèces, et plus localement entre l'immigration et l'extinction locale (Fig. i.4). Avec peu de paramètres, il est capable de reproduire divers patrons observés de distribution et d'abondance d'espèces (Bell 2001; Etienne 2007). Cette théorie est dite neutre parce qu'elle ne prend pas en compte les différences de niches ou de traits entre espèces d'un même niveau trophique, les considérant négligeables par rapport aux évènements de reproduction et de mort qui sont considérés comme stochastiques. Cette théorie a mis en valeur l'importance des dimensions spatiale et temporelle, en incluant la dispersion, qui était jusqu'alors peu prise en compte dans les modèles de différenciation de niche, et la spéciation, quasiment absente des théories de coexistence.

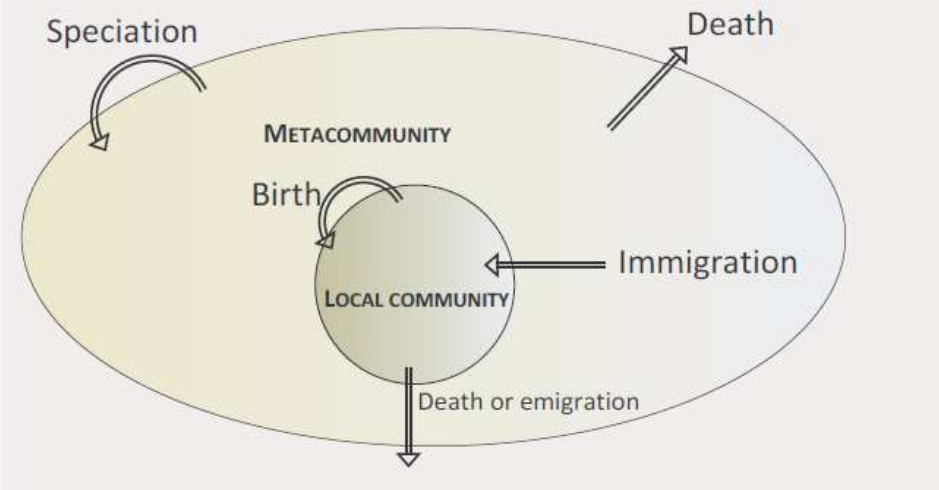

Fig. i.4. Le modèle neutre de Hubbell le plus cité. Un certain nombre d'individus sont en compétition pour la même ressource (ex. nutriments, lumière, espace) et sont contraints par une équation : si un site se libère, suite à la mort d'un individu, un nouvel individu, issu de la reproduction, le colonise. L'hypothèse de neutralité fait que tous les individus ont la même probabilité de colonisation que leur descendance : soit ils ont beaucoup de descendants qui ont une faible capacité de colonisation, soit ils en ont peu mais ceux-là ont une forte capacité de colonisation.

Ce modèle a d'abord suscité une vive critique (Clark *et al.* 2007). Toutefois, le nouveau regard qu'il a apporté a permis de revisiter la théorie de la niche, incluant la dispersion (Kneitel & Chase 2004) ou même des processus démographiques stochastiques (Tilman 2004). Les visions contemporaines de la théorie de niche (Chase 2005) reconnaissent que les différenciations de niches écologiques peuvent être temporelles (phénologie, perturbation, démographie), spatiales (répartition des ressources), concerner les réseaux d'interactions (parasitisme, prédation) ou le type de ressource. Le principal problème est devenu celui de choisir les mécanismes les plus importants pour la coexistence dans le système étudié, parmi une multitude de possibilités

La dispersion, un processus central

La théorie neutre a mis en avant l'importance capitale de la dispersion pour la coexistence des espèces. La réconciliation des deux théories de coexistence des espèces a ouvert la voie aux analyses comparant l'importance de la dynamique spatio-temporelle générée par la dispersion à l'importance de la différenciation de niches (Kneitel & Chase 2004; Gravel *et al.* 2006; Holyoak *et al.* 2006). La dispersion des espèces agit à diverses échelles et influence la coexistence à travers plusieurs mécanismes. La dynamique source-puits va permettre à une espèce de se maintenir là où elle devrait être exclue par la compétition ou parce que les conditions abiotiques ne lui sont pas favorables (Pulliam 2000; Soberon 2007). La limitation de la distance de dispersion aboutit à une concentration des individus de l'espèce, augmentant la compétition intra-spécifique et favorisant la coexistence (Holyoak *et al.* 2006). Il en résulte des effets variés sur la diversité, agissant parfois dans des directions opposées (Cadotte & Fukami 2005), qui sont difficiles à résumer par de simples facteurs explicatifs.

La dispersion, qui se divise en trois phases (émigration, transfert, établissement), est un processus difficile à isoler en cela qu'il dépend de beaucoup d'autres. La phase d'émigration est sensible aux conditions environnementales lors du développement de l'espèce (ex. manque de ressources), et aux conditions environnementales avoisinantes. Elle

dépend donc de la structure spatiale des habitats favorables au développement de l'espèce. L'efficacité du transfert est affectée par la santé des matures (ex. taille des plantes), les habitats alentours (structure et identité), et par la présence des vecteurs pour la dispersion passive (ex. oiseaux), qui vont déterminer la distance de dispersion. Enfin, la phase d'établissement dépend des conditions environnementales dans le lieu d'arrivée. La dispersion est donc un processus central très sensible aux changements directs et indirects du climat (Travis *et al.*, voir annexe 6). Les changements de vents peuvent affecter par exemple la distance de dispersion des graines (Simmons & Thomas 2004). Les impacts peuvent être aussi indirects. Le climat peut agir sur le développement des plantes et leur taille adulte peut varier en conséquence, diminuant la distance de dispersion des graines (Zhang *et al.* 2012).

Une vision hiérarchique et multi-échelles des mécanismes

Pour expliquer la présence d'une espèce à un endroit donné Il est évident que plusieurs facteurs agissent à différents niveaux d'organisation des écosystèmes, impliquant des mécanismes variés. Tout d'abord, le pool d'espèces disponibles doit être restreint en considérant l'histoire biogéographique de la région. Les processus de spéciation et d'extinction mais aussi les glaciations, les volcans, et la dérive des continents, peuvent expliquer en grande partie les patrons de richesse d'espèces au niveau du globe (Wiens & Donoghue 2004). Ensuite, les facteurs abiotiques comme le climat sont souvent suffisants pour expliquer la présence ou l'absence d'une espèce sur de vastes étendues géographiques (Guisan *et al.* 1998). Les contraintes abiotiques agissent comme un premier filtre qui délimite les conditions dans lesquelles l'espèce peut s'établir, étant donné ses capacités physiologiques (Fig. i.5). La capacité de dispersion constitue un deuxième filtre, permettant aux espèces d'avoir accès aux sites où l'environnement abiotique leur est favorable (Fig. i.5).

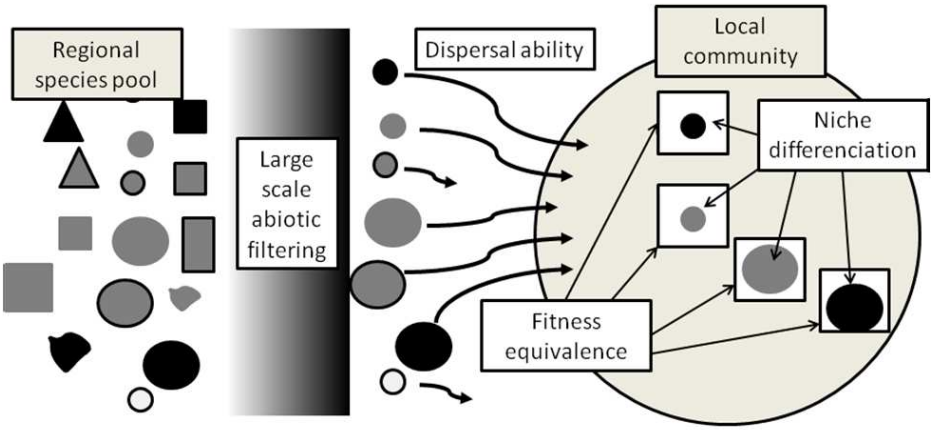

Fig. i.5. Hiérarchie spatiale des processus. Le pool régional d'espèces est déterminé par l'histoire biogéographique de la région. Il est tout d'abord filtré par les conditions abiotiques qui exercent une forte contrainte sur la présence des espèces. Ensuite, seules les espèces qui peuvent atteindre les sites favorables sont retenues. Enfin, au niveau de la communauté, la coexistence peut être le résultat de niches différentes ou bien, si l'on considère une échelle spatio-temporelle supérieure, de processus neutres.

C'est au niveau de la communauté locale, où les interactions entre espèces ont lieu, que les mécanismes de coexistence vont être les plus difficiles à dissocier. L'importance de la dispersion, par exemple, dépend de la structure du paysage, de la répartition spatiale des espèces et de leurs mouvements, ainsi que des dynamiques temporelles (Cadotte & Fukami 2005). Le challenge est d'isoler les mécanismes qui ont lieu localement en prenant en compte l'influence des mécanismes agissant aux échelles supérieures et en retirant leurs effets (Thuiller *et al.* 2010a annexe 2). La question est de savoir si la performance des espèces, par exemple mesurée par leur abondance, est le résultat de leur position le long d'un gradient environnemental et de la compétition qui en résulte, où bien des dynamiques liées à la dispersion. Si un ou plusieurs axes de différenciation de niche entrent en jeu, il s'agit ensuite de pouvoir les identifier. Le Chapitre II de cette thèse se propose de palier à ce manque de connaissance par la prise en compte des trois facteurs clés expliquant la présence et l'abondance des espèces (environnement abiotique, dispersion et interactions biotiques).

DE LA DIVERSITE SPECIFIQUE A LA DIVERSITE FONCTIONNELLE

Les limites de l'approche taxonomique

Mesurer la biodiversité et son évolution en dénombrant les espèces est soumis à beaucoup plus d'approximations que l'on pourrait penser a priori. Tout d'abord, connaitre l'exclusivité des espèces présentes dans une région est quasiment impossible (Hughes *et al.* 1997). De plus, on découvre continuellement de nouvelles espèces, y compris chez les

mammifères (Ceballos *et al.* 2005). Enfin la description et la classification des taxons ne sont pas une tâche facile. Le concept d'espèce le plus répandu est basé sur l'isolement reproductif. Ernst Mayr (Mayr 1940) définit les espèces comme des *« groupes de populations naturelles, effectivement ou potentiellement interfécondes, qui sont génétiquement isolées d'autres groupes similaires, et qui peuvent engendrer une descendance viable et féconde ».* Ce concept, né d'une réflexion sur les oiseaux, n'est pas forcément adapté à d'autres organismes. Chez les plantes par exemple, les hybridations entre espèces sont fréquentes et rendent particulièrement complexe leur classification. Quand il n'y a pas de reproduction sexuée (ex. bactéries) cette définition d'espèce atteint rapidement ses limites. D'autres mesures de biodiversité que celles uniquement basées sur la richesse en espèces doivent donc être envisagées.

Du concept d'espèce à celui de groupe fonctionnel

En 1859, Darwin reconnaissait déjà que le concept d'espèce était flou : « *Jusqu'à présent, on n'a pas pu tracer une ligne de démarcation entre les espèces et les sous-espèces, c'est-à-dire entre les formes qui dans l'opinion de quelques naturalistes pourraient être presque mises au rang des espèces sans le mériter tout à fait ; on n'a pas réussi davantage à tracer une ligne de démarcation entre les sous-espèces et les variétés fortement accusées ou entre les variétés à peine sensibles et les différences individuelles*. » (L'origine des espèces). Cette idée de continuité des différences entre individus aux différences entre espèces peut être prise en compte lorsque l'unité de base n'est plus l'espèce, mais l'individu. Tout à fait cohérente avec cette notion, l'écologie fonctionnelle, plus particulièrement développée pendant les 20 dernières années, propose de décrire les organismes par leurs caractéristiques biologiques et leurs fonctions au sein de l'environnement (Calow 1987). Ces caractéristiques, les traits fonctionnels, sont mesurables et comparables entre espèces (d'un même niveau trophique) et ont un impact sur la survie, la croissance ou la reproduction de l'individu (Violle *et al.* 2007). Dans l'idéal, pour détecter et étudier des mécanismes assez fins et s'affranchir totalement

du concept d'espèce, la mesure des caractères devrait être faite au niveau des individus (Albert *et al.* 2010a; Albert *et al.* 2012 annexe 4). En pratique, lorsque le nombre d'espèces et de populations étudiées devient trop important, on a recours aux valeurs moyennes de traits, mesurée à partir de quelques individus, et que l'on attribue ensuite à l'espèce et toutes à ses populations indifféremment. La variabilité intra-spécifique peut néanmoins être non négligeable (Albert *et al.* 2010a), et l'approximation des traits individuels par une moyenne est donc une forte contrainte sur le niveau de détail que l'on peut considérer dans les analyses et les modèles. Cependant, pour des espèces suffisamment contrastées, les différences interspécifiques permettent tout de même de distinguer les principales stratégies fonctionnelles (Albert *et al.* 2010a). Basés sur un jeu de traits fonctionnels non-redondants et bien choisis, on peut alors définir des groupes fonctionnels (Lavorel *et al.* 1997) qui caractérisent les principales stratégies et les rôles fonctionnels des espèces au sein de l'écosystème. Dans certains modèles, ces unités peuvent remplacer les espèces (Woodward & Diament 1991; Albert *et al.* 2008) puisque dans certains cas peu nous importe l'identité taxonomique des espèces, ce sont leurs fonctions qui nous intéressent.

Toutefois, jusqu'à présent, une certaine dichotomie persiste entre les écologistes travaillant sur les traits fonctionnels, ceux travaillant sur la théorie de la coexistence et ceux modélisant les espèces. Ces trois sous champs disciplinaires sont néanmoins complémentaires et peu de travaux ont cherché à mixer les trois approches. Les groupes fonctionnels définis en réponse aux changements globaux (Lavorel *et al.* 1997) ne font pas explicitement le lien avec les mécanismes de coexistence implémentés dans les modèles de distribution (ex. niche abiotique). D'un autre côté, les groupes fonctionnels destinés aux modèles, lorsqu'ils font le lien avec la niche climatique, ne prennent pas en compte des traits liés à la dispersion (ex. Laurent *et al.* 2004). Finalement, une proposition de groupes fonctionnels basés sur les mécanismes de coexistence ne prend pas en compte le processus de filtre abiotique (Herault 2007). Une approche intégrative combinant les trois points de vue serait donc un développement majeur pour

l'écologie. De tels groupes fonctionnels, basés à la fois sur des traits nécessaires à la coexistence des espèces, des traits impliqués dans leur réponse aux gradients environnementaux, et compatibles avec les modèles, rendraient possible une nouvelle rencontre entre l'écologie fonctionnelle et la modélisation de la biodiversité (voir chapitres III et IV).

L'approche fonctionnelle, un pont entre l'individu et l'écosystème

Les traits fonctionnels permettent de relier les caractéristiques des individus à celui des écosystèmes (Shipley 2007). Par exemple, Garnier *et al.* (2007) ont montré comment les traits peuvent être utilisés pour prédire la réponse des individus, des communautés et des écosystèmes aux changements d'utilisation des terres. Ils ont notamment mis en relation les traits foliaires comme la teneur en matière sèche (TMSF ou LDMC), indicatrice de la stratégie d'exploitation des ressources (Wright *et al.* 2004), avec des propriétés des écosystèmes comme la décomposition des litières et l'accumulation de biomasse, qui sont impliquées dans les processus comme les cycles du carbone et de l'azote. Deux mécanismes, basés sur les traits, peuvent expliquer la relation entre la diversité et le fonctionnement des écosystèmes. Lorsque la diversité est grande, la probabilité d'occurrence d'une modalité ou valeur de trait importante pour une fonction de l'écosystème augmente (Crawley *et al.* 1999). Dans ce cas, l'identité fonctionnelle est importante. La deuxième explication est l'effet de complémentarité (Loreau 1998). Si la divergence fonctionnelle est élevée, la variété de traits permet une diversité d'exploitation des ressources, c'est-à-dire qu'un grand nombre de niches est occupé, et l'utilisation des ressources atteint une efficacité maximale. Les mesures de diversité fonctionnelle qui prennent en compte les traits des espèces, permettent donc de faire le lien entre la diversité et le fonctionnement des écosystèmes (Diaz & Cabido 2001). Par exemple, la valeur moyenne des traits foliaires et racinaires au niveau d'une communauté de plantes explique une grande partie de la fertilité du sol (Diaz *et al.* 2007).

C'est grâce à ces propriétés que la modélisation de groupes fonctionnels pourra représenter les caractéristiques des écosystèmes (chapitre III). La modélisation dynamique de ces groupes fonctionnels (chapitre IV) sera une voie vers la prédiction de l'évolution des propriétés des écosystèmes et des services qu'ils fournissent.

MODÉLISER, L'ART DU COMPROMIS

La modélisation est une façon de représenter la nature, en la simplifiant pour comprendre les phénomènes, faire des prédictions, et éventuellement agir sur les phénomènes. La modélisation est nécessaire pour tester des hypothèses et en formuler de nouvelles. Richard Levins, dans son article « *The Strategy of Model Building in Population Biology* » (Levins 1966), est l'un des premiers à présenter les problèmes fondamentaux concernant la construction de modèles. Son point de vue a largement influencé les biologistes depuis 50 ans. Il part du postulat que la construction de modèles, qu'ils soient théoriques, mathématiques ou informatiques, implique nécessairement une simplification des phénomènes et fait appel à des compromis. Un modèle doit inclure les aspects les plus importants selon l'objectif et l'état des connaissances. En effet, l'approche de 'force brute' consistant à représenter chacun des éléments du système étudié par un modèle mathématique fidèle n'a pas de sens pour trois raisons : les données sont limitées, la résolution mathématique serait trop compliquée, et l'interprétation serait impossible.

Levins décrit trois qualités d'un modèle : la généralité, le réalisme et la précision. Etant donné qu'il est difficile d'inclure ces trois propriétés dans un même modèle, Levins propose trois types de compromis. Les modèles qui abandonnent l'objectif de généralité demandent beaucoup de données et de connaissances, et s'appliquent à un système particulier, mais sont précis et réalistes. Ils permettent de comprendre en détail les mécanismes qui aboutissent au patron observé, et peuvent être utilisés pour faire des prédictions robustes. Les modèles sacrifiant le réalisme sont par exemple des équations générales, des lois. Ils peuvent être utiles pour réaliser des prédictions sans accumuler

beaucoup de données, mais pas pour comprendre les phénomènes en détail. Les derniers modèles, peu précis, retiennent particulièrement l'attention de Levins. En effet, lorsque la quantification des phénomènes n'est pas importante, cette solution offre la possibilité de construire des modèles réalistes et généraux, qui permettent de comprendre assez bien les phénomènes et prédire leur tendance générale.

Le principal objectif de notre approche de modélisation sera de déterminer les facteurs les plus importants (chapitre II) pour pouvoir extraire l'essentiel. Nous appliquerons ce principe dans le chapitre III, où la diversité végétale sera réduite à son essence fonctionnelle, et lors du développement du modèle FATE-H (chapitre IV), où seuls les principaux mécanismes seront pris en compte.

Deux autres idées fondamentales moins connues sont apportées par Levins. Tout d'abord, il incite les approches multiples et complémentaires, toutes étant partiellement fausses et incomplètes, en écrivant que *'la vérité se trouve à l'intersection de mensonges indépendants'*. Il présente aussi l'idée d'emboitement de modèles à différentes échelles, chacun apportant une justification des paramètres suffisants pour le niveau supérieur. Notre approche de modélisation sera basée sur la combinaison de modèles, où chacun agit à une échelle différente. Par exemple, le mécanisme de filtre biotique sera modélisé par un premier modèle, et ses sorties deviendront l'entrée des modèles de succession décrivant les processus locaux (Chapitre IV).

CADRE METHODOLOGIQUE

LES MESURES DE DIVERSITE SPECIFIQUE ET FONCTIONNELLE

La biodiversité peut être mesurée à chaque niveau (habitat, espèces, gènes, traits) par deux composantes. La richesse correspond au nombre de catégories différentes du système étudié (ex. nombre d'espèces ou habitats, différentes valeurs de traits) et l'équitabilité mesure la régularité de la distribution des effectifs associés à chaque catégorie (Whittaker 1965). Les indices couramment utilisés permettent de prendre en compte l'abondance des espèces et donc évaluer à la fois la richesse et l'équitabilité. Whittaker (1960) a proposé de considérer trois niveaux de diversités emboitées, α, β et γ. Les diversités α et γ sont semblables, la diversité α étant mesurée localement et la diversité γ étant la diversité totale du système étudié. Il a été montré que tous les différents indices proposés depuis MacArthur (Macarthur 1955) sont des mesures d'entropie :

$$H = \sum_{i=1}^{S} p_i \,.g(p_i)$$

S est le nombre d'espèces, p_i l'abondance relative de l'espèce i et g une fonction d'information décroissante. Si $g(p_i) = (1-p_i)/p_i$, H est la richesse spécifique. Si $g(p_i) = -ln(p_i)$, H est l'indice de Shannon et si $g(p_i) = 1-p_i$, H est l'indice de Simpson. La formule d'entropie généralisée de Tsallis (1988) permet de synthétiser ces résultats mais celle proposée par Hill (1973), est particulièrement intéressante car elle permet une appréhension plus intuitive de la notion de diversité :

$${}^{q}D = \left(\sum_{i=1}^{S} p_i^{q} \right)^{1/(1-q)}$$

q est l'ordre de diversité. Les indices de Shannon et Simpson sont des simples transformations des nombres de Hill, d'ordre respectif $q=1$ et $q=2$. Un nombre de Hill, ou *« nombre d'espèces équivalentes »* ou

encore *« nombres d'espèces efficaces »*, de valeur X, peut être interprété comme la diversité d'une communauté de X espèces équitablement distribuées (i.e. de même abondance).

La diversité β est en général dérivée des deux premières (Whittaker 1960) et mesure le taux de changement entre différentes localités. Il y a plusieurs manières de la définir et de l'interpréter (Tuomisto 2010), selon les mesures utilisées pour α et γ et leur façon d'être combinées ($\beta = \gamma/\alpha$ ou $\beta = \gamma-\alpha$). La décomposition qui est la plus consistante est celle qui implique les nombres de Hill et une approche multiplicative. Dans ce cas, β peut être interprété comme un nombre d'espèces équivalentes et correspond à la *« vraie diversité »* (Jost 2006; Tuomisto 2010; Tuomisto 2011).

En ce qui concerne la diversité fonctionnelle, une notion supplémentaire entre en compte, celle de similarité (ou dissimilarité) entre espèces (ou individus). Une dissimilarité est toujours positive entre deux individus différents et elle est nulle entre un individu et lui-même. Pour définir une distance, il faut que la dissimilarité vérifie aussi la propriété d'inégalité triangulaire ($d_{ij} \leq d_{ik} + d_{kj}$). Étant donné que les traits fonctionnels peuvent être quantitatifs, qualitatifs (ordonnés ou non) et présenter des données manquantes, la mesure de distance la plus utilisée est celle de Gower (1971) étendue par Podani (1999). Elle calcule la dissimilarité entre deux individus par la moyenne des dissimilarités calculées pour chaque trait, dont la valeur est comprise entre 0 et 1. Pour une variable quantitative, la différence de valeur entre deux espèces est normalisée par l'étendue des valeurs de la variable. Les variables ordonnées sont remplacées par leur rang et traitées comme les variables quantitatives. La dissimilarité vaut 0 ou 1 pour des variables qualitatives, et les valeurs manquantes sont simplement ignorées. Afin de prendre en compte les distances dans les mesures de diversité, l'entropie quadratique de Rao (Q) est intéressante parce qu'elle offre un cadre général (de Bello *et al.* 2010a) :

$$Q = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j = 1 - \frac{1}{{}^2D}$$

d_{ij} est la distance entre l'espèce i et l'espèce j. En outre, l'entropie quadratique est une simple transformation des nombres de Hill d'ordre $q=2$ (Jost 2006; Tuomisto 2010a), ce qui permet de calculer la « vraie » diversité fonctionnelle β (Voir Chapitre I).

LES ASSEMBLAGES D'ESPECES ET L'ECOLOGIE DES COMMUNAUTES

La condition principale pour le maintien de la biodiversité est la coexistence des espèces qui ont une écologie similaire, dans la même région. Ces espèces sont donc dans un même niveau trophique et utilisent les mêmes ressources (Chesson 2000a). Si la coexistence fait clairement référence à des situations où la persistance des espèces considérées est infinie, on se basera la plupart du temps sur l'observation de simples cooccurrences à un moment donné. Les données de base utilisées dans ce cas sont des relevés de communautés, où la quasi-totalité des espèces à été notée, ainsi que, dans certains cas, leurs abondances approximatives. L'objectif de ces relevés est de se placer à l'échelle où les espèces interagissent, afin d'identifier et de comprendre les mécanismes qui permettent leur coexistence et qui expliquent la structure des communautés.

Les propriétés étudiées sont par exemple la diversité de la communauté, la distribution des traits ou des abondances relatives des espèces, la productivité et d'autres propriétés impliquées dans le fonctionnement des écosystèmes. Par exemple, la hiérarchie des filtres environnementaux (Fig. i.6) peut être testée. Les facteurs qui ont des variations régionales (ex. température) devraient plutôt déterminer la valeur de trait moyenne de la communauté, résultat du premier filtre abiotique. Les variables agissant localement devraient permettre la différenciation de niches et influenceraient plutôt la distribution des traits des espèces dominantes. Cette hypothèse a été validée empiriquement dans la vallée de la Guisane (Hautes-Alpes, France)

pour des communautés végétales (de Bello *et al*., voir annexe 5). Dans d'autres cas, les analyses peuvent se placer dans un contexte de méta-communautés (plusieurs communautés connectées par la dispersion), afin d'évaluer l'importance relative de la structure spatiale et de l'environnement abiotique (ex. Meynard *et al.* Annexe 7).

Mettre en évidence l'importance relative de la compétition, de la dispersion et de l'environnement abiotique pour expliquer les assemblages d'espèces peut avoir des applications directes, comme par exemple la gestion des invasives (Thuiller *et al.* 2010a), mais reste un challenge. La dispersion est souvent représentée par un terme d'auto-corrélation spatiale (ex. Borcard *et al.* 1992), sans aucune relation à la capacité de dispersion de d'espèce. Cette approche limite fortement l'interprétation de l'importance du terme spatial. La compétition est un mécanisme qui est particulièrement difficile à détecter (Voir chapitre II). Son effet est mesurable à l'intérieur de la communauté seulement, et il est mélangé à celui des variables abiotiques locales. L'enjeu est donc de choisir la dimension spatiale appropriée, les bonnes métriques, un modèle nul qui permettra d'isoler le mécanisme à tester, notamment en retirant les effets des facteurs agissant à plus large échelle, et une mesure de similarité de niche entre deux espèces pertinente, tout en étant adaptée aux connaissances et aux données accumulées (Thuiller *et al.* 2010a). Une approche sera proposée dans le chapitre II pour analyser l'importance relative de l'environnement abiotique, de la dispersion et des interactions biotiques sur la présence et l'abondance locale d'une espèce.

MODÉLISER LA BIODIVERSITÉ : VERS UNE APPROCHE DYNAMIQUE

Des modèles basés sur les filtres abiotiques régionaux

L'approche biogéographique pour comprendre et prédire la présence d'une espèce à un endroit donné est basée sur la relation espèce-milieu. Les progrès informatiques de ces dernières décennies ont permis aux scientifiques d'utiliser de grandes bases de données pour mettre en relation les présences observées des espèces avec le climat, qui est

connu depuis De Candolle (1955) comme étant un facteur de premier ordre pour expliquer la répartition de nombreuses espèces. Les méthodes statistiques concernées ont été largement développées (Guisan & Thuiller 2005; Heikkinen *et al.* 2006; Elith & Leathwick 2009; Thuiller *et al.* 2009) et ces modèles, dit « *d'habitat* », ont été utilisés extensivement, que ce soit pour prédire la réponse des espèces aux changements environnementaux (Thuiller *et al.* 2006a; Beaumont *et al.* 2011) ou l'évolution de la diversité fonctionnelle (Thuiller *et al.* 2006b) ou phylogénétique (Thuiller *et al.* 2011).

L'approche est basée sur le concept de niche grinnelliennne (environnement abiotique), et sa projection dans l'espace géographique. Cependant, la répartition observée de l'espèce résulte également des conditions biotiques et des mécanismes de dispersion (Soberon 2007). Hutchinson (1957) est le premier à distinguer deux types de niches grinnelliennes. La niche dite « *fondamentale* » est déterminée par les conditions environnementales tolérées en l'absence d'interactions biotiques. La niche dite « *réalisée* » correspond aux conditions environnementales dans lesquelles l'espèce est effectivement observée, résultat des interactions biotiques, de la limitation par la dispersion et d'autres mécanismes (ex. source-puits). Les modèles d'habitat estiment la niche réalisée des espèces, et présentent donc des limites évidentes pour la projection dans des situations biotiques ou des configurations spatiales différentes (Guisan & Zimmermann 2000; Thuiller *et al.* 2008). Cette approche reste cependant très intéressante à une certaine échelle où les interactions biotiques sont négligeables, et sera la base de nombreux autres modèles.

Approches multi-espèces et interactions biotiques

Lorsqu'il s'agit de modéliser la distribution de plusieurs espèces en même temps, pour mesurer ensuite la biodiversité, plusieurs approches sont utilisées. Tout d'abord, les modèles d'habitat peuvent être appliqués à un très grand nombre d'espèces, mais n'incluent pas les mécanismes de dispersion ni d'interactions biotiques. Ils ne permettent

donc pas de prendre en compte la dynamique de la répartition des espèces.

D'un autre côté, de nombreux modèles mécanistes de dynamique de la végétation (DVM) ont été développés. Ils prennent en compte la dynamique temporelle des espèces, en incluant parfois la démographie, la compétition et/ou la dispersion (ex. LAMOS, Cousin *et al.* 2003, LPJ, Sitch *et al.* 2003). La plupart d'entre eux sont cependant restreints à la végétation dominante et projettent les changements d'habitats ou de biome sur de larges échelles spatiales, et ont peu d'utilité à l'échelle régionale (Harrison *et al.* 2010). De plus, ils sont souvent limités à une dizaine de types fonctionnels de plantes (PFT) parce qu'ils nécessitent trop de données, de connaissance et de temps de calcul, et ne sont donc pas capables de modéliser directement des changements de biodiversité.

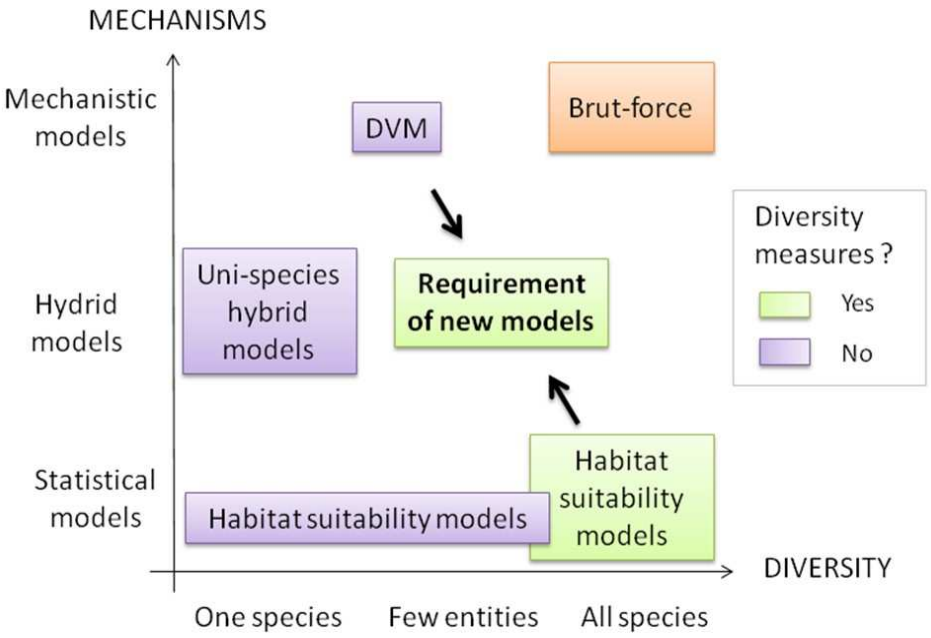

Fig. i.6 La place des nouveaux modèles de la dynamique de la biodiversité. Un modèle dynamique de biodiversité doit impliquer un minimum d'entités de modélisation pour représenter une diversité. Il doit aussi comporter des mécanismes décrivant la dynamique des espèces. Une approche hybride peut permettre de dépasser les limites existantes en combinant les avantages d'un modèle mécaniste et d'un modèle statistique. DVM=modèle dynamique de végétation.

Nous mettons en évidence ici un manque de modèles dynamiques multi-espèces, capables de modéliser l'évolution spatio-temporelle de la biodiversité. L'objectif principal de cette thèse est le développement d'un tel modèle (Chapitres III, IV et V).

Approches hybrides uni-espèce

Dans le but d'inclure un maximum de mécanismes dans les modèles de biodiversité, tout en considérant la limite des données et des connaissances disponibles, des approches hybrides sont nécessaires (Fig. i.6). Etant donnée la hiérarchie des facteurs expliquant la répartition spatiale des espèces (Fig. i.5), les rares exemples de couplage de modèles combinent un modèle d'habitat où les facteurs abiotiques (ex. climat, sol) sont pris en compte alors que la démographie, la compétition et/ou la dispersion des espèces sont modélisées par une approche mécaniste (Wintle *et al.* 2005; Keith *et al.* 2008; Anderson *et al.* 2009). Cette combinaison de modèles comporte toutefois quelques problèmes à résoudre (Gallien *et al.* 2010, voir annexe 1), notamment concernant la forme et la force de la relation entre le modèle d'habitat et les autres modèles. Dans la plupart des cas, ces choix sont justifiés par la connaissance d'experts et/ou selon le principe de parcimonie. Les paramètres influencés par l'habitat sont par exemple le nombre d'individus par unité de surface (Keith *et al.* 2008; Anderson *et al.* 2009) ou la survie et/ou la fécondité (Wintle *et al.* 2005; & Thuiller 2008; Dullinger *et al.* 2009), et la relation est généralement linéaire ou logistique. Cependant, les rares expériences ou analyses sur le sujet ont montré que le lien entre habitat et performance n'est pas évident, les relations étant même parfois opposées à celles attendues (Wright *et al.* 2006; Thuiller *et al.* 2010b).

Model name	**Sub-model types**	**Organisms**	**Reference**
RAMAS-GIS	HS +SEMM	South african fynbos	Keith *et al.* 2008
MigClim	HS + Spread model	Plants	Engler & Guisan 2009
x	HS + Spread model	Argentine ant	Roura-Pascual *et al.* 2009
SPAnDX	HS + IBM	Acacia nilotica	Kriticos *et al.* 2003

Tab. i.1 Quelques exemples de modèles hybrides. A chaque fois, un modèle d'habitat est couplé à un modèle dynamique.

HS=habitat suitability model ; IBM=individual-based model ; SEMM=spatially explicit metapopulation model

Modéliser la dynamique de la biodiversité

Afin de modéliser la dynamique de la biodiversité, l'enjeu est de représenter la diversité des espèces en utilisant un nombre suffisant d'entités de modélisation (Fig. i.6), qu'il soit aussi possible de paramétrer. Un tel modèle pourrait projeter d'autres composantes de la biodiversité que la richesse en espèce, comme par exemple la diversité des habitats, ou la diversité fonctionnelle. Les modèles hybrides qui ont été développés jusqu'à maintenant sont principalement destinés à comprendre et prédire la répartition d'une espèce cible mais l'approche de combinaison de modèle peut être appliquée aux modèles de végétation (Hickler *et al.* 2004 et Chapitre IV et V).

Notre objectif est de pouvoir modéliser des entités qui puissent représenter la biodiversité à l'échelle régionale. Nous utiliserons pour cela le modèle dynamique de la végétation de BIOMOVE (Midgley *et al.* 2010) et nous le développerons. Ce modèle (FATE-H) est un couplage entre un modèle d'habitat et un modèle de succession végétale. Il a principalement été utilisé sur de petites échelles spatiales et pour un très petit nombre de groupes fonctionnels (ex. Albert *et al.* 2008). Notre objectif est de l'utiliser pour modéliser la dynamique du paysage à l'échelle régionale, en utilisant des groupes fonctionnels qui représentent la diversité et la structure de la végétation dominante. Le modèle peut aussi combiner un module de dispersion, que l'on développera pour nos groupes fonctionnels, et un module de perturbation. Il permettra donc de prédire l'évolution de la végétation en fonction du climat et de l'utilisation des terres (chapitre V).

La dispersion dans les modèles

L'enjeu d'inclure plus de connaissance sur la dispersion dans les modèles est grand puisque c'est un processus central, fondamental pour la dynamique spatiale et temporelle. Aujourd'hui, la dispersion est principalement prise en compte par des fonctions de dispersion qui sont calibrées sur les patrons observés de répartition des populations (Tab. i.2 & Travis *et al.* annexe 6). Cette approche phénoménologique ne permet pas de comprendre la dépendance de la dispersion à la qualité de

l'habitat ou à la démographie de l'espèce et produit donc des prédictions peu robustes. L'enjeu est d'inclure la dispersion de manière plus mécanistique, en prenant en compte les phases d'émigration, de transfert, et d'établissement de l'espèce. Quelques modèles existent déjà (ex. PATCH, SPAndX), où plus de mécanismes sont intégrés (Tab. i.2). Nous chercherons à prendre en compte la dispersion dans son ensemble dans le modèle de dynamique de végétation développé au cours de cette thèse (chapitre IV).

Model type	**How dispersal is implemented**	**Example**	**Model name**
Niche-based model	Full dispersal/ no dispersal	Thuiller *et al.* 2011 (European plants, birds and mammals)	Biomod
Landscape model	Species specific dispersal kernels based on species mean dispersal distances	Lischke *et al.* 2006 (Swiss trees)	TreeMig
Landscape model	Seed dispersal kernel based on effective and maximum dispersal distances.	Scheller *et al.* 2008 (New Jersey Pine Barrens)	LANDIS
Migration model	All cohorts optimize their position according to their possible interactions with all other cohorts.	Saltré *et al.* 2009 (*Fagus sylvatica*)	Gibbs-based model
Cellular automaton	Jump-dispersal events based on distance and habitat quality	Roura-Pascual *et al.* 2009 (Argentine ant)	Spread model
	Probability function based on dispersal distance, landscape and time since colonization	Engler & Guisan 2009	MigClim
Spatially explicit metapopulation models	Incidence functions	Keith *et al.* 2008 (South african fynbos),	RAMAS-GIS
Spatially explicit Individual Based population model	Animals search for suitable and unoccupied breeding sites within minimal and maximal distances using random walks	Schumaker *et al.* 2004 (species in the Oregon's Willamette basin)	PATCH
Hybrid model	Seed dispersal probability affected by livestock and presence of watercourses	Kriticos *et al.* 2003 (Acacia nilotica)	SPAnDX

Tab. i.2
Implementation de la dispersion dans plusieurs types de modèles.

OBJECTIFS GENERAUX DE LA THESE ET ORGANISATION

L'objectif principal de la thèse est de caractériser les espèces et les habitats vulnérables aux changements climatiques et d'utilisation des terres dans les Alpes Françaises. La démarche utilisée consiste à (1) déterminer les mécanismes et les facteurs les plus importants pour expliquer la présence et l'abondance des espèces (2) utiliser ces connaissances pour adapter un modèle de dynamique de la végétation puis le valider (3) Utiliser ce modèle pour construire des scenarios, qui pourront éventuellement servir d'aide à la décision.

(1)Décrire et Analyser les patrons de rareté et d'abondance

Chapitre I. Niche breadth, rarity and ecological characteristics of the French Alps flora. *Article publié dans Journal of Biogeography (Janvier 2012)*

Ce premier chapitre explore la spécialisation des plantes dans les Alpes à partir de la cooccurrence des espèces au niveau de la communauté. La largeur de niche ainsi déterminée est mise en relation avec d'autres mesures de rareté et des traits qui représentent des stratégies fonctionnelles.

Chapitre II. Accounting for dispersal and biotic interactions in order to disentangle the drivers of species distributions and their abundances. *Article publié dans Ecology Letters (online)*

Ce chapitre propose un modèle hiérarchique pour analyser l'importance relative du filtre abiotique, de la dispersion et des interactions biotiques (directes ou indirectes) sur la présence et l'abondance d'une espèce.

(2)Modéliser la végétation à l'échelle d'un espace naturel protégé

Chapitre III. Optimizing plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. *Article soumis à Global Change Biology*

Dans ce chapitre, l'objectif a été de construire des groupes fonctionnels capables de représenter la structure des communautés et d'être paramétrés pour un modèle dynamique de végétation. Ces groupes ont été construits à partir d'une poignée de traits qui représentent les principaux mécanismes à l'origine de la structure des communautés (Fig. i.7). Leur capacité à mesurer la diversité a été évaluée.

Chapitre IV. Fate-h: a spatially and temporally explicit hybrid model for predicting the vegetation structure and diversity at regional scale. *Article en préparation pour Journal of Applied Ecology.*

Le développement d'un modèle hybride de dynamique de végétation (FATE-H), qui puisse reproduire les patrons de structure et de diversité de la végétation, a été validé dans ce chapitre, sur le territoire du Parc national des Ecrins.

(3)Prédire le futur de la diversité de la végétation dans les Ecrins

Chapitre V. Consequences of climate and land use change on the vegetation structure and diversity in the Ecrins National Park. *Article en préparation.*

Ce chapitre explore les futurs possibles de la végétation du parc national des Ecrins, selon deux scenarios de pâturage contrastés. L'interaction de ces scenarios avec un changement climatique est aussi examinée.

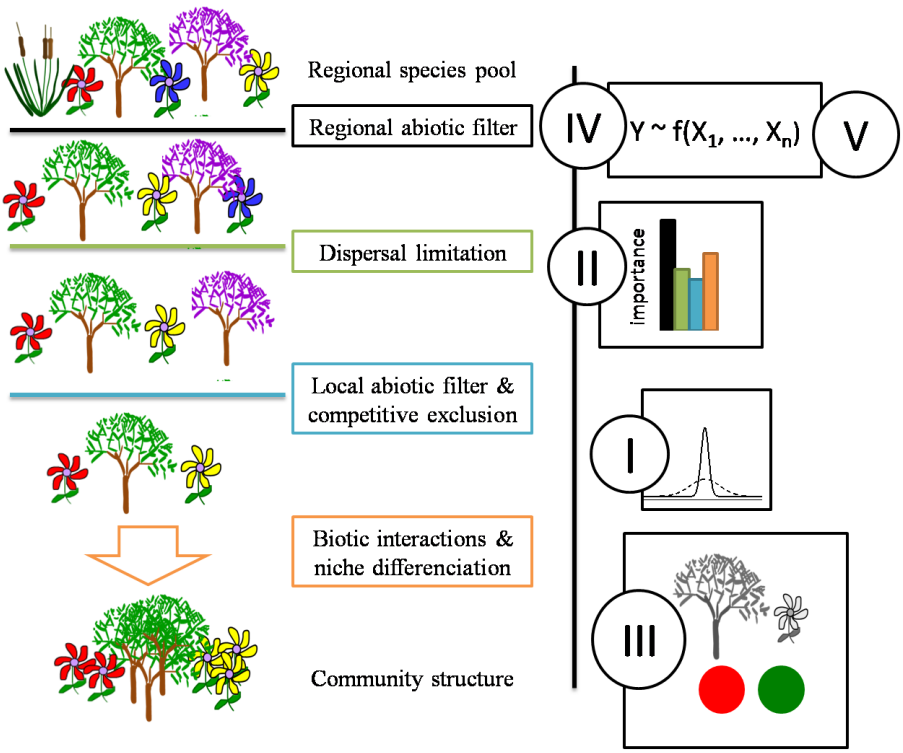

Fig. i.7. Représentation schématique de la place des chapitres par rapport au cadre conceptuel.

CADRE BIOGEOGRAPHIQUE ET ECOLOGIQUE

Toutes les études présentées dans les chapitres qui suivent se sont focalisées sur les Alpes françaises et sa végétation. La suite présente quelques éléments qui caractérisent cette région, les plantes qui y vivent et le Parc National des Ecrins, sur lequel se sont concentrés les derniers chapitres.

LES ALPES FRANÇAISES

Une diversité climatique à l'origine d'une importante biodiversité

La principale particularité des écosystèmes montagnards est leur gradient altitudinal et leur topographie complexe, responsable de larges variations climatiques sur de très courtes distances. Cette forte hétérogénéité spatiale de l'environnement, combinée aux diverses influences climatiques (Fig. i.8), est à l'origine de la grande diversité d'espèces que l'on peut trouver dans les Alpes (Körner 1999). Nous pouvons y observer par exemple environ 2/3 de la flore Française (voir aussi Fig. i.9).

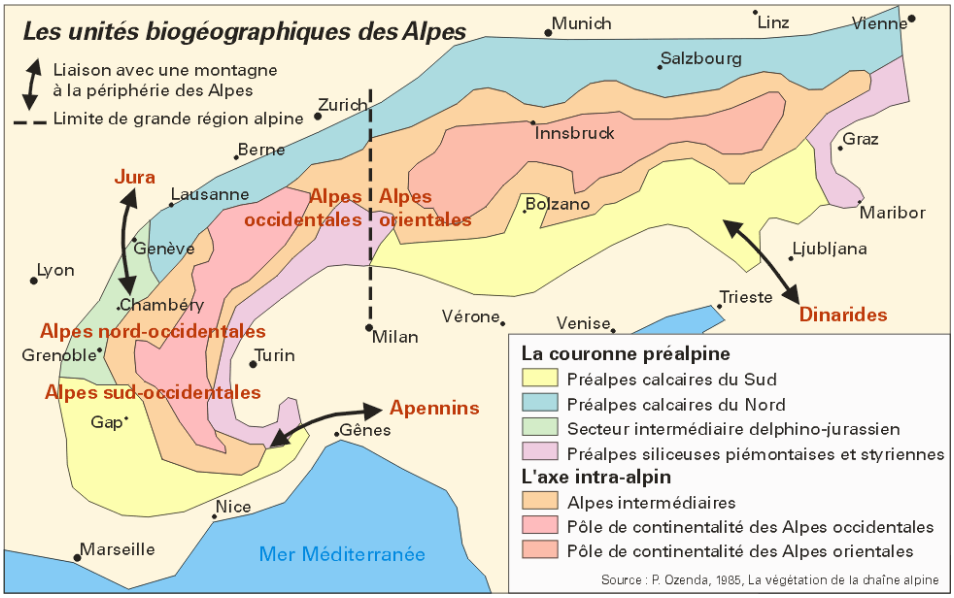

Fig. i.8 Les unités biogéographiques dans les Alpes. Les Alpes Françaises sont à cheval sur 4 types biogéographiques. Les pré-Alpes calcaires du Sud et le secteur intermédiaire delphino-jurassien forment les « Alpes externes ». A l'Est des Alpes intermédiaires se trouvent les Alpes occidentales continentales appelées aussi « Alpes internes ».

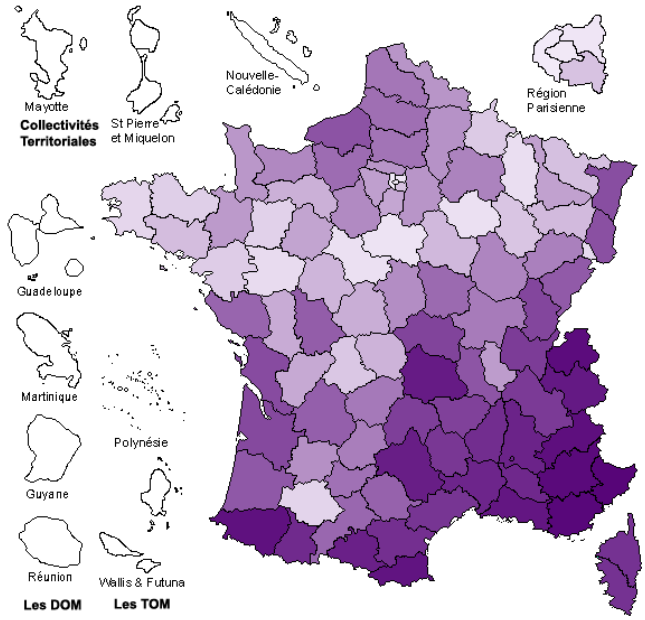

Fig. i.9 La diversité taxonomique des plantes en France. Le gradient de couleur mauve représente le nombre de taxons observés dans chaque département (du plus clair au plus foncé). Les Alpes, au sud-est, concentrent plusieurs départements où le nombre d'espèce est important. Source : Tela Botanica.

Histoire des perturbations anthropiques dans les Alpes

En montagne, dans les Alpes, les principaux changements environnementaux sont liés aux pratiques agricoles et forestières, et plus récemment au tourisme, à la pollution azotée et aux espèces envahissantes. Dès le Néolithique, les premiers bergers transhumants provoquaient des incendies à la limite altitudinale de la forêt. Ensuite, il y a eu des déforestations successives de l'époque romaine au Moyen Age (Girel 2006). Au début du XIXe siècle, l'activité agricole de la région était étendue, avec de l'élevage et des cultures variées (cdg05.fr),

mais la majorité des zones qui étaient labourées et fauchées à l'étage subalpin sont aujourd'hui des zones de pâturage (Clément *et al.* 2003). Cette déprise agricole, généralisée en zone de montagne, est encore la tendance actuelle, même si le Parc National des Ecrins s'efforce de maintenir la fauche dans quelques prairies (ex. Col du Lautaret). La forêt a donc recolonisé naturellement les terres cultivables abandonnées, mais elle a aussi gagné de l'espace grâce au reboisement. Néanmoins, dans les années 70, le développement du tourisme avec l'arrivée des stations de ski a apporté une nouvelle vague de déboisement. La répartition actuelle des forêts s'explique donc par l'histoire de l'utilisation des terres plutôt que par le climat (Gehrig-Fasel *et al.* 2007).

LA VEGETATION DE MONTAGNE

Les plantes comme sujet d'étude

Les plantes offrent plusieurs avantages à être étudiées. Elles constituent un niveau trophique central, étant la ressource de nombreux organismes. De plus, les espèces dominantes structurent le paysage, créant les habitats pour de nombreuses autres espèces. La végétation est par conséquent centrale dans l'évaluation de la biodiversité. D'autre part, la botanique est une discipline ancienne, qui est partagée par de nombreux passionnés (16892 inscrits à Tela Botanica, France), et dont les connaissances sont assez développées. De nombreuses bases de données sont donc disponibles sur la répartition et les caractéristiques de beaucoup d'espèces végétales.

Les plantes sont regroupées de plusieurs façons selon leurs stratégies fonctionnelles. La classification des types biologiques selon Raunkiaer (1934) est particulièrement intéressante parce qu'elle représente les principales différences démographiques (Chapin III *et al.* 1996; Lavorel *et al.* 1997; Lavorel & Garnier 2002). Elle regroupe les plantes selon la manière dont elles protègent leurs bourgeons pendant la mauvaise saison (Fig. i.10):

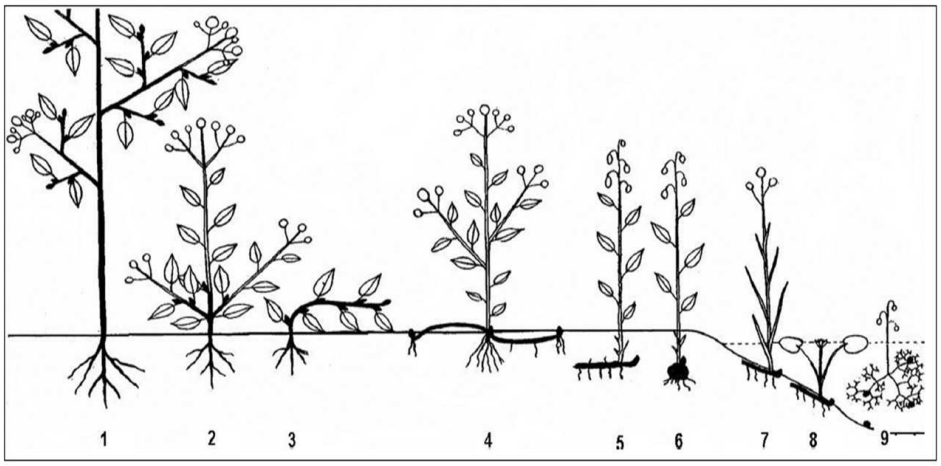

Fig. i.10. Principaux types biologiques selon Raunkiaer. Les *Phanérophytes* (**1**) ont des bourgeons dormants aériens à plus de 50 cm de la surface du sol. Les *Chamaephytes* ont des bourgeons dormants aériens à moins de 50 cm de la surface du sol. Ils peuvent être frutescents (**2**) ou herbacés (**3**) Les *Hémicryptophytes* (**4**) ont des bourgeons dormants à la surface du sol. Ils développent ensuite une touffe de pousses, une rosette de feuilles ou une tige érigée. Les *Géophytes* ont des bourgeons dormants sous la surface du sol (bulbe (**6**), tubercule, ou rhizome (**5**)). Les *Hydrophytes* : (feuilles immergées, **8**) et les *Hélophytes* (feuilles émergées, **7**) ont des bourgeons dormants sous l'eau.

Aux altitudes supérieures, les plantes sont soumises à des conditions extrêmes et ont mis en place des stratégies particulières. Les annuelles, qui dépendent exclusivement du succès de la reproduction sexuée, sont remplacées par des espèces pérennes, souvent clonales (Körner 1999). La présence d'une banque de graines en dormance permet aux quelques annuelles d'attendre la meilleure année pour germer. Certaines plantes comme la renoncule des glaciers (Fig. i.11) préforment leurs bourgeons des années à l'avance pour optimiser l'utilisation des conditions favorables à la floraison (Aubert SAJF).

(a) **(b)** **(c)**

Fig. i.11. Quelques plantes Alpines. **(a)** *Androsace helvetica*, pérenne en coussin **(b)** *Geum reptens*, rhizomateuse d'altitude **(c)** *Ranunculus glacialis*, très résistante au froid. Photos : Isabelle Boulangeat, 2008.

La répartition des plantes et le climat

La répartition des plantes est fortement liée à la température et aux précipitations. Le réchauffement climatique a par exemple pour effet la remontée en altitude de la limite des aires de répartition des espèces (Randin *et al.* 2009a). Ce changement dans la distribution des habitats a pour conséquence de réduire la surface disponible pour les espèces qui colonisent des altitudes supérieures puisque les conditions environnementales se décalent vers les sommets (Jump *et al.* 2012).

Les conditions climatiques peuvent être déterminantes sur des distances très courtes. Par exemple, les combes à neiges et leurs crêtes voisines, éloignées de l'ordre du mètre, présentent des espèces caractéristiques qui ont des stratégies d'adaptation très contrastées (Fig. i.12). Les plantes de crêtes ont besoin de feuilles épaisses pour supporter les conditions extrêmes (pleine lumière, vent, gel) tandis que les plantes de combes sont protégées par la neige mais n'ont qu'un temps très réduit pour fini leur cycle de vie (Choler 2005). La présence du manteau neigeux va donc avoir des effets importants sur la phénologie des espèces et leur survie. Ici, nous ne nous intéresserons pas directement à l'effet du manteau neigeux, en général supposé grossièrement pris en compte par des variables climatiques et topographiques.

Fig. i.12 Combes et crêtes. On peut voir à cette époque de l'année (début juillet) que certaines combes sont encore sous la neige. A l'inverse, les crêtes sont dégarnies depuis longtemps, et sont peu végétalisées. Photo : Isabelle Boulangeat, 2008.

La coexistence des espèces végétales en montagne

Lorsqu'on applique les théories de coexistence des espèces aux plantes, il faut garder à l'esprit quelques particularités de ces organismes. Les espèces végétales sont sessiles et la majorité d'entre elles ont une dispersion à courte distance (Vittoz & Engler 2007; Dullinger *et al.* 2011). D'autre part, les plantes ont deux modes de reproduction qui peuvent être complémentaires : la reproduction sexuée et la reproduction végétative. La dispersion est donc particulièrement

difficile à décrire. D'une part, à courte distance, la clonalité peut jouer un rôle important par rapport à la dispersion des graines (Alexander *et al.* 2012). D'autre part, la distance de dispersion des graines est très variable d'une espèce à l'autre (ex. dispersion par les grands mammifères et dispersion sans vecteur), et la dispersion longue distance est mal connue (Vargas *et al.* 2012).

En ce qui concerne les interactions biotiques, les ressources sont quasiment les mêmes pour toutes les plantes (eau, nutriment, lumière, Silvertown 2004). La différenciation de niche ne concernera pas ou peu la nature des ressources mais plutôt la manière d'exploiter ces ressources, par exemple sur un gradient de stratégies d'acquisition-conservation (Diaz *et al.* 2004; Wright *et al.* 2004). La stratégie d'acquisition efficace des ressources (forte capacité photosynthétique, croissance rapide) s'oppose à celle de la conservation des ressources (tissus denses, croissance lente). D'autre part, dans les Alpes, les interactions biotiques peuvent changer avec les conditions environnementales. Plusieurs études ont montré que lorsqu'on approche les altitudes les plus hautes où l'environnement devient particulièrement stressant (froid intense, vent), la facilitation entre espèces augmente (Callaway *et al.* 2002; Choler 2005). Au contraire, à basse altitude, dans les milieux où les ressources sont abondantes, la compétition entre plantes est forte et pourrait mener à l'exclusion de certaines espèces (Zimmermann *et al.* 2009).

LE PARC NATIONAL DES ECRINS

Un parc national d'Europe

En Europe, les parcs nationaux sont très différents de ceux d'Amérique du Nord, conséquence de leur longue histoire d'utilisation des terres. L'activité de l'homme, à travers les guerres, les migrations de population, les fluctuations démographiques et économiques, a profondément modifié les paysages européens, si bien qu'à la fin du XIXème siècle, on ne trouve presque plus d'espaces inexploités en Europe. L'influence de l'homme n'a pas systématiquement détruit la

biodiversité, mais au contraire a façonné une mosaïque de milieux qui abritent aujourd'hui une multitude d'espèces. L'objectif des Parc Nationaux de France est principalement d'entretenir la diversité créée par les sociétés rurales traditionnelles avant la révolution industrielle. Ils ont aussi vocation à protéger des sites d'une beauté exceptionnelle et qui abritent de nombreuses espèces emblématiques et sont enfin des territoires privilégiés pour la recherche scientifique et pour le développement d'une gestion durable des activités humaines.

Caractéristiques générales du Parc National des Ecrins

Les premières zones qui ont été protégées dans ce parc sont situées dans la vallée de la Bérarde et datent de 1913. Les agrandissements successifs ont aboutis à la création du Parc National des Ecrins le 27 mars 1973. Il s'étend sur deux départements (Hautes-Alpes et Isère), sur une superficie de 178 400 hectares, entre 669 et 4102 mètres d'altitude. Il comporte trois types de zones avec différents statuts de protection (Fig. i.13). Les réserves intégrales dédiées à des expérimentations scientifiques sont fermées au public. La zone centrale (50% de la superficie), où les espèces et les milieux sont protégés, est strictement réglementée mais autorisée au public et à certaines activités agricoles. Elle inclue quelques villages d'altitude avec seulement trois habitants permanents. La zone périphérique est une zone d'animation et d'interactions avec les populations locales, où vivent environ 30 000 habitants toute l'année.

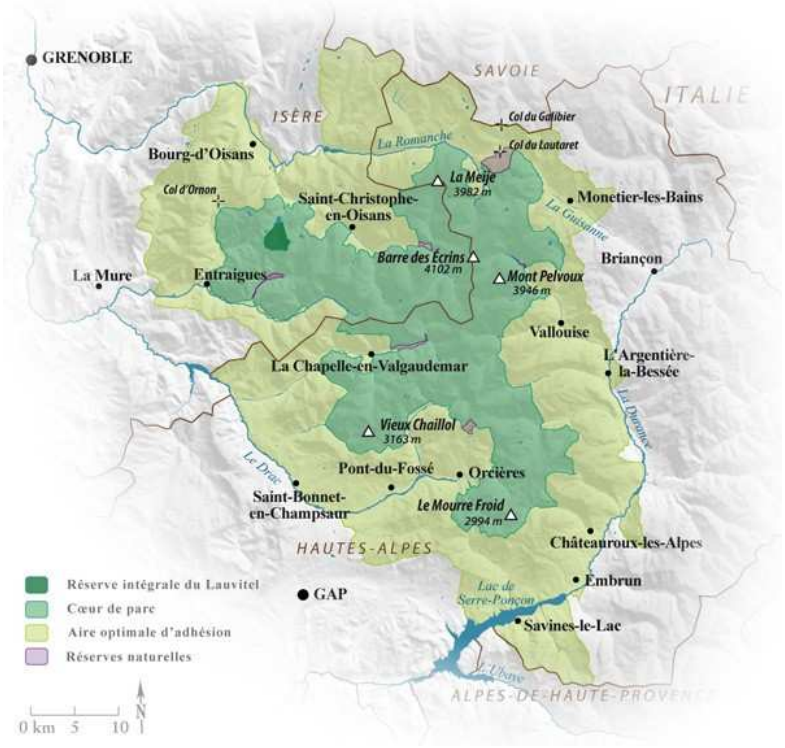

Fig. i.13 Le parc national des Ecrins. Il est situé dans le Sud Est de la France, non loin de la frontière Italienne et de Grenoble. Il est divisé en trois zones de statut de protection différent. La zone centrale (cœur de parc), la zone périphérique (aire optimale d'adhésion) et la réserve intégrale. La zone périphérique n'a pas de statut de protection particulier. Source : site des Parc Nationaux de France.

La végétation du Parc National des Ecrins

La flore du parc comporte environ 2000 espèces dont 216 répertoriées comme rares ou menacées et 350 endémiques dont 146 sont protégées. Ses habitats sont principalement des espaces ouverts (Fig. i.14) qui constituent 60% de la surface totale, pour seulement 24% de forêts. Le reste du Parc est dénué de toute végétation (glaciers et neiges éternelles). Les essences forestières naturelles (non plantées) caractéristiques sont, dans les Alpes externes, le sapin (*Abies alba*) et le hêtre (*Fagus sylvatica*), et dans les Alpes internes le pin sylvestre (*Pinus sylvestris*) et le mélèze (*Larix decidua*) (Fig. i.15).

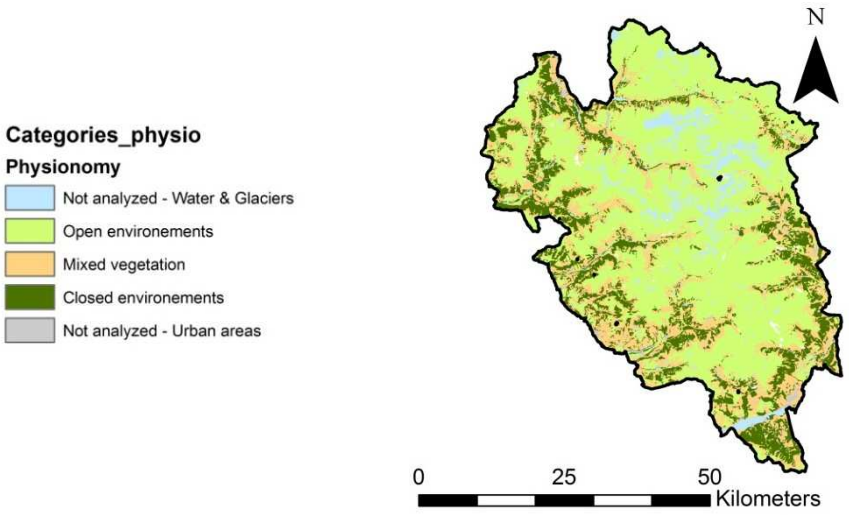

Fig. i.14 Espaces ouverts et fermés dans le parc national des Ecrins. . Source : à partir des données de l'atlas Delphine, Parc des Ecrins.

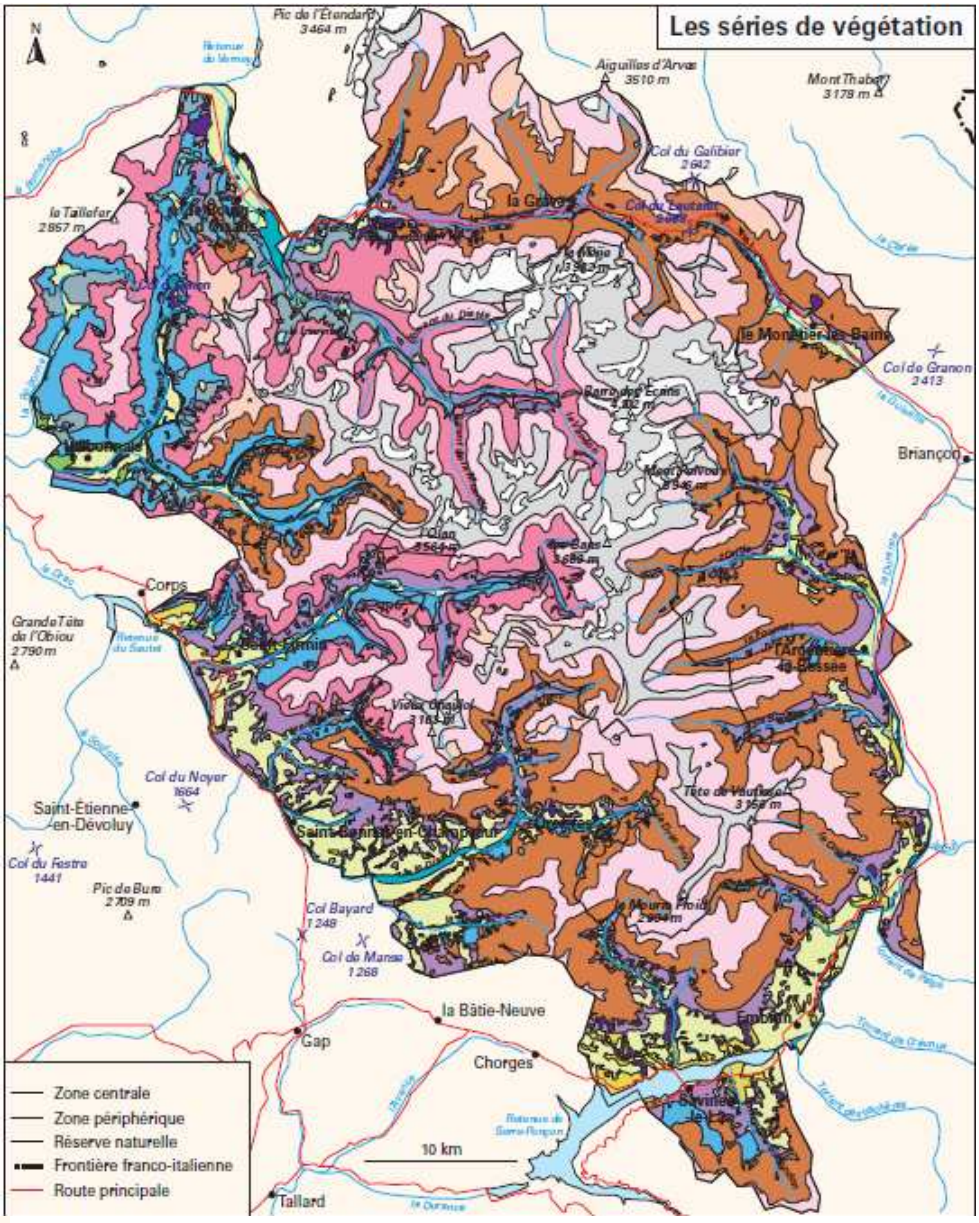

Fig. i.15 Séries de végétation dans le parc national des Ecrins. Les séries de végétation représentent la végétation attendue si l'homme n'avait pas d'impact sur le milieu. Le choix des couleurs affectées à chaque série de végétation traduit les conditions climatiques de la série de végétation, du bleu pour l'humidité au rouge pour la sécheresse. Source : Atlas du Parc National des Ecrins.

QUELQUES ÉLÉMENTS SUR LES DONNÉES PRINCIPALES

Dans les Alpes Françaises, le protocole de relevés utilisé en masse est celui de Braun-Blanquet (1946). Dans une zone où la végétation est homogène, pouvant varier de 9m² à 10000m² selon les types de milieux, jusqu'à quatre strates de hauteur sont définies et toutes les espèces sont relevées avec leur classe d'abondance (selon le pourcentage de couverture de leur strate). Les classes d'abondance sont logarithmiques : moins de 1%, de 1 à 5%, de 5 à 25% de 25 à 50% de 50 à 75% et plus de 75%. Dans la majorité des études, la stratification n'est pas prise en compte, ni le pourcentage de sol nu (donné par strate). L'échantillonnage des espèces annuelles et des espèces rares, petites et de couleurs ternes est sujet à de fortes incertitudes, selon l'année et la date du relevé, sans compter l'expertise de l'observateur. Cette courte description du protocole de relevé des espèces permet d'avoir une idée des incertitudes associées aux données et des limites de leur précision. Néanmoins, on dispose dans les Alpes Françaises de plus de 10000 de ces relevés (Fig. i.16), qui ont été échantillonnés après 1980 et qui ont subi un premier « contrôle qualité » prenant en compte la précision de la localisation, l'expertise des observateurs, l'homogénéité du milieu et les incertitudes taxonomiques. Malgré une information incomplète sur la surface des relevés, une deuxième sélection a été effectuée dans les études qui suivent, afin de retirer les relevés atypiques. Puisque la végétation d'un relevé est homogène, on peut toutefois supposer raisonnablement que les individus des espèces assez abondantes (>25%) se trouvent très proches, à l'échelle où la coexistence a encore un sens.

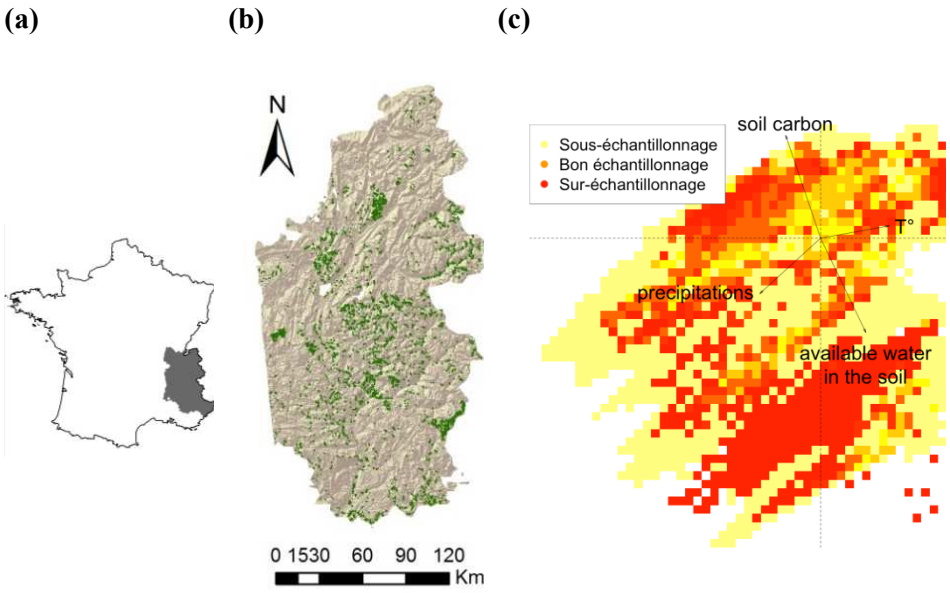

Fig. i.16. La répartition des relevés dans la zone d'étude. 8160 relevés ont passé les différentes sélections de qualité. Réalisés entre 1980 et 2009, ils n'ont pas fait l'objet d'un plan d'échantillonnage élaboré. On peut voir ici que la pression d'échantillonnage est très hétérogène spatialement. Cela se traduit aussi sur le plan climatique. **(a)** Situation de la zone d'étude en France **(b)** Répartition spatiale des relevés. **(c)** Répartition des relevés sur le plan climatique directeur. Ce plan est le premier d'une analyse en composantes principales, impliquant 6 variables abiotiques et tous les pixels de la zone.

CHAPITRE I:

NICHE BREADTH, RARITY AND ECOLOGICAL CHARACTERISTICS WITHIN A REGIONAL FLORA SPANNING LARGE ENVIRONMENTAL GRADIENTS

Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L. Thuiller, W. (2012) Niche breadth, rarity and ecological characteristics within a regional flora spreading over large environmental gradients. *Journal of Biogeography*, **39**, 204-214

Author contributions: I.B., S.L. and W.T. designed the study; L.G and J.VE collected the data and helped to interpret it; and I.B. ran the analyses and wrote the paper with substantial contributions from W.T. and S.L.

Editor: Ole Vetaas

Abstract

Aim Species specialization, which plays a fundamental role in niche differentiation and species coexistence, is a key biological trait in relation to population responses to changing environments. Species with a limited niche breadth are considered to experience higher extinction risks than generalist species. This work aims to measure the degree of specialization in the regional flora of the French Alps and test whether species specialization is related to species rarity and ecological characteristics.

Location This study was conducted in the French Alps region, which encompasses a large elevational gradient over a relatively limited area (26,000 km^2).

Methods Specialization was estimated for approximately 1200 plant species found in the region. Given the inherent difficulty in pinpointing the critical environmental niche axes for each individual species, we used a co-occurrence-based index to estimate species niche breadths (specialization index). This comprehensive measurement included crucial undetermined limiting niche factors, acting on both local and regional scales, and related to both biotic and abiotic interactions. The specialization index for each species was then related to a selection of plant typologies such as Grime strategies and Raunkiaer life forms, and to two measurements of plant rarity, namely regional area of occupancy and local abundance.

Results Specialist species were mainly found in specific and harsh environments such as wetlands, cold alpine habitats and dry heathlands. These species were usually geographically restricted but relatively dominant in their local communities. Although none of the selected traits were sufficient predictors of specialization, pure competitors were over-represented amongst generalist species, whereas stress-tolerant species tended to be more specialized.

Main conclusions Our results suggest that co-occurrence-based indices of niche breadth are a satisfactory method for inferring plant specialization using large species samples across very heterogeneous environments. Our results are an empirical validation of the tolerance–dominance trade-off and also provide interesting insights into the long-standing question of which biological properties characterize species with narrow niche breadth that are potentially threatened by global changes in the environment.

INTRODUCTION

The functioning of ecosystems involving complex interactions is strongly altered by ongoing global changes (Chapin, 2000; Thuiller, 2007), and may lead to unprecedented biodiversity losses (Pimm & Raven, 2000). However, not all species or ecosystems are expected to have the same vulnerability (Sala *et al.*, 2000). Some regions, such as alpine regions, are considered as 'biodiversity hotspots' (Körner, 2004) because they harbour numerous rare or specialist species expected to be particularly sensitive to extinction (Pimm *et al.*, 1988; Gaston, 1997).

Species specialization, resulting from evolutionary trade-offs between a species' ability to exploit a wide range of resources and the effectiveness with which it uses each of these, may provide indicators of species response to global changes in the environment (Gregory *et al.*, 2005; Broennimann *et al.*, 2006; Winck *et al.*, 2007). Apart from rare exceptions recorded in highly arid climates where environmental changes may favour specialist species over generalist species (Attum *et al.*, 2006), those with limited environmental tolerance and resource use spectra are expected to be more sensitive to environmental changes than generalists (Evans *et al.*, 2005; Wilson *et al.*, 2008). This has recently been shown for a large range of individual taxa including plants (Thuiller *et al.*, 2004a), birds (Jiguet *et al.*, 2007; Devictor *et al.*, 2008a), fish (Munday, 2004; Feary, 2007), mammals (Laidre *et al.*, 2008) and bumblebees (Williams, 2005). Conversely, generalist species are expected to dominate as a result of habitat fragmentation or anthropogenic disturbance (for an example on birds, see Devictor *et al.*, 2008b).

Ecological specialization is one of the main mechanisms of niche differentiation, which in turn favours species coexistence (Chase & Leibold, 2003). A species' niche is usually defined as the *n*-dimensional environmental space occupied by a species along different environment axes (Hutchinson, 1957). As formulated in Gause's law, two species competing for the same resource cannot coexist if all other ecological factors remain constant. One scenario that may explain observed

patterns of diversity is that one of the two species initially competing for similar resources escapes from competitive exclusion by specializing in a small part of the multi-dimensional ecological space. This species becomes more competitive in this restricted ecological space where it may dominate, to the detriment of other parts of the gradient where it becomes a weaker competitor and may even be excluded. Specialist species are therefore expected to have a high local relative abundance and to occur in peculiar or stressful environments such as high elevations, wetlands or xeric habitats (Thompson *et al.*, 1998; Lavergne *et al.*, 2004). These patterns would be explained by a tolerance–dominance trade-off across species (Wisheu, 1998).

A range of metrics for measuring niche specialization have been applied in ecological studies (Devictor *et al.*, 2010). For instance, specialization has been inferred indirectly from species distributions and environmental data (Thuiller *et al.*, 2004a), from direct measurements of species performance in multiple environments (Kassen, 2002), or from detailed measurements of species diets, such as variance in prey size (Bolnick *et al.*, 2003). All these methods require the pre-selection of the main factors limiting resource acquisition (Austin *et al.*, 1984; Austin, 1985). However, niche differentiation based on a few selected resource-limiting axes does not seem to explain plant coexistence as most plants require common resources (light, water, CO_2, phosphorus, potassium and certain othermineral nutrients) and there are a limited number of ways in which they can acquire them (Silvertown, 2004). There is increasing evidence that numerous axes of niche differentiation are needed to explain species coexistence (Clark *et al.*, 2007), particularly in species-rich communities such as herbaceous habitats. Given the lack of understanding of the key environmental variables that determine each species' niche and the paucity of reliable spatial data on all potential environmental variables, the description of a species' niche is generally based on the few niche axes that are relatively easy to measure or to gather from spatial datasets (Vetaas, 2002; Chase & Leibold, 2003). To investigate niche specialization over a large set of species and a large spatial scale whilst accounting for niche axes that

explain coexistence at the community scale, we chose a metric that does not require any pre-selection of environmental variables. Fridley *et al*. (2007) proposed using the co-occurring species to depict diversity across a given species' habitats. They consider that '*Co-occurrence data offer an approach that is in effect a biological assay for 'habitat diversity' or 'niche width' that requires no assumptions about the definition of a habitat or the most critical environmental factors that control plant species distributions'* (Fridley *et al.*, 2007, p. 708). This indirectly accounts for numerous niche axes that may be of importance at both local and regional scale, and which may differ from one species to another.

Here, we use an extensive vegetation survey across the French Alps region that encompasses a broad elevation gradient from 55 to 3200 metres a.s.l., and investigate the overall pattern of plant niche specialization for more than 1200 plant species. The study region provides an optimal ecological setting for studying plant specialization as it presents steep environmental gradients over small spatial scales (Körner, 1999). We specifically address the following questions: (1) Do specialist species occur in particular habitats? (2) Is species specialization related to their geographical range and local dominance? (3) Which biological characteristics are common among specialist species?

MATERIALS AND METHODS

Data

This study was conducted over the French Alps region (Fig. 1), which covers over 26,000 square kilometres and presents a wide range of environmental conditions due to mixed continental, oceanic and Mediterranean climatic influences, with annual precipitation ranging from 522 to 2895mm, mean annual temperatures ranging from -7 to 12.6 °C and slope angle up to 78° (data extracted from the meteorological model Aurelhy (Bénichou and Le Breton, 1987), based on interpolated measurements at a resolution of 250x250m). We used a

comprehensive vegetation survey of 6929 community plots sampled over large environmental gradients from 55 to 3200 m a.s.l. (from lowlands to alpine summits). For each plot the relative abundance of all present species was recorded, for a total of 2543 species overall. The National Alpine Botanic Conservatory (CBNA) provided this dataset. Plots were surveyed in a homogeneous area of 100m^2 in average. Smaller habitats had a minimum of 10m^2 and some forest plots were sampled up to 1000m^2. Species nomenclature was standardized according to the *Index synonymique de la flore de France* (Kerguélen, 1993).

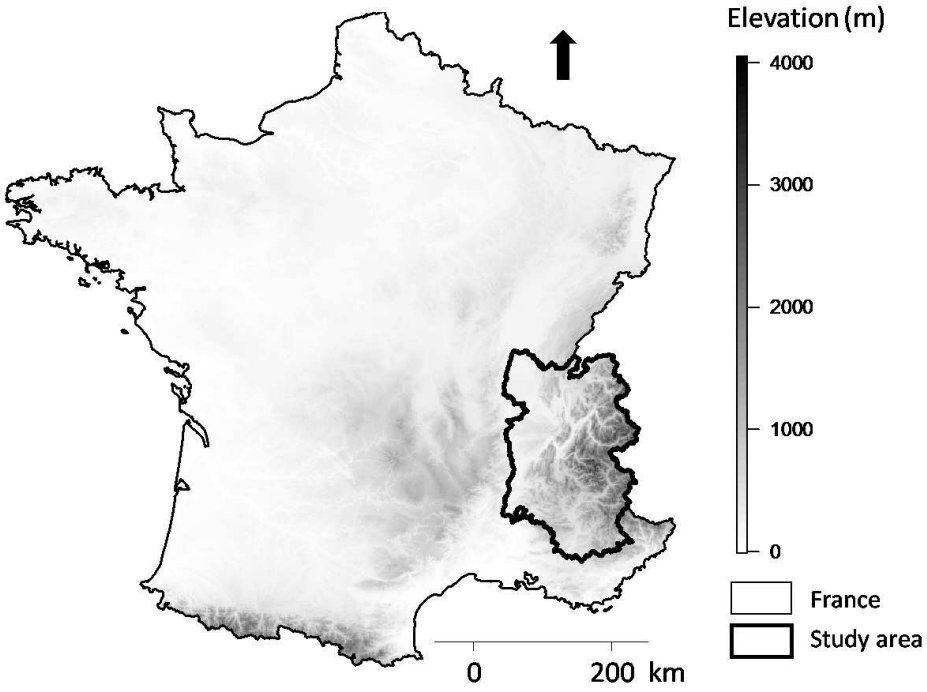

Figure I.1 The study area of the French Alps region, located in the south-east of France. This area is on the edge of the Alpine region, where three climatic zones come together: the Mediterranean, continental and oceanic climates.

Each plot was assigned to one of ten habitat classes. Forests were subdivided into evergreen and deciduous forests. Six herbaceous habitats were described: meadows (including tall grass prairies, usually mown), grasslands (mostly grazed), rocks (cliffs and screes), wetlands (marshes, swamps, stream edges, peat bogs), floodplains and fields (cultivated areas). Two other classes described shrub habitats: the first represented scrubland including garrigue and heathlands (open land with low shrubs such as *Rhododendron ferrugineum* or *Vaccinium myrtillus*), and the second class contained thickets.

Studied species were assigned to different Grime ecological strategies (*sensu* Grime, 1974) for 891 species (competitor, ruderal, stress-tolerator or mixed), life span for 864 species (annual/biennial, perennial herbs, perennial woody species) and life forms for all species (Raunkiaer's classification, Raunkiaer, 1934). This was done using the field observations of botanists from the Alpine Botanical Conservatory and two available databases: LEDA (Knevel *et al.*, 2003) and BiolFlor (Kühn *et al.*, 2004).

Methods

In order to estimate plant specialization, we used the co-occurrence index 'theta' proposed by Fridley *et al.* (2007). The overall method relies on the assumption that the species found in many different habitats (i.e. generalists) have a relatively high rate of species turnover across the plots in which they occur. Reciprocally, specialist species, regardless of their frequency in the data set, should have a low species turnover in their plots because they consistently occur within the same set of species (Fridley *et al.*, 2007). The general idea is very similar to indirect species ordination such as (detrended) correspondence analysis (DCA; ter Braak, 1987). However, this recently developed method makes it possible to include a re-sampling procedure that accounts for differences in species frequencies in the dataset and makes it possible to select the appropriate underlying distance and turnover (beta) diversity metrics. This last point seems crucial given the recent literature on beta diversity estimation (de Bello *et al.*, 2010a; Tuomisto, 2010a,b; Anderson *et al.*, 2011). To ensure the method is comprehensive, we provided a comparison of species niche breadth estimates using the theta index (Fridley *et al.*, 2007), an indirect gradient ordination, DCA (ter Braak, 1988) and a direct gradient ordination, outlying mean index (OMI) (see Table S1 in Appendix S1 in the Supporting Information).

The overall frequency of a species in the sampled plots results from both the vegetation survey sampling strategy and the species' niche specialization. Following the framework proposed by Fridley *et al.* (2007), we removed the effects of the sampling design in the dataset by

applying a randomization procedure. We randomly chose a fixed number of plots containing the focal species before calculating the turnover among these plots, thereby keeping the plot frequency constant between species. For each species we applied the randomization 100 times. Theta is the resulting average turnover. We also calculated the standard deviation of turnover from these 100 repetitions.

The number of selected plots for each randomization had to be determined arbitrarily, based on the number of species present in the vegetation database but also on the minimum number for species occurrence. Setting the threshold too high (e.g. > 40 plots) removed too many species with few occurrences, whereas setting the threshold too low affected the relevance of the measure. We selected a threshold of 10 plots after having checked that the results were consistent for 5, 10 and 15 plots (see Table S2 in Appendix S1). Furthermore, we decided to only calculate theta for species occurring in more than 20 plots in order to be able to resample the plots for all the species analysed. Species occurring in fewer than 20 plots were, however, kept in the community data to compute the theta value for all other species. The specialization index was thus computed for 1216 plant species.

The most critical point of this approach is the estimation of the species turnover among the sampled plots. Fridley *et al.* (2007) originally proposed using the additive beta measure [$\beta = \gamma - \mu(\alpha)$], where γ is the total number of species in the 10 sampled plots and $\mu(\alpha)$ is the mean species richness of these 10 plots. This choice was recently criticized on the grounds that this beta measure 'is dependent on the size of species pool at the position of species optima' (Manthey & Fridley, 2009; Zelen´y, 2009). Another set of possible measurements was then proposed including the Jaccard index, two other indices based on Simpson or Sørensen for multiple sites (Baselga *et al.*, 2007) and one based on R.H. Whittaker's decomposition. Based on the recommendations, we could still use several indices according to what we aim to measure. In the recent literature, several authors attempted to gather all these beta diversity indices into a more comprehensive framework in order to guide ecologists in their choices (Jost, 2006,

2007; de Bello *et al.*, 2010a; Tuomisto, 2010a,b; Anderson *et al.*, 2011). In light of all these discussions, we chose an index that estimates the proportional species turnover between plots and that generalizes the methodological framework, allowing the inclusion of species abundances and functional or phylogenetic dissimilarities between species if available. This index is based on Rao's quadratic entropy formula (Rao, 1982):

$$Q = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j \quad (1)$$

where S is species richness, d_{ij} is the dissimilarity between each pair of species i and j (equal to 1 when $i \neq j$ or 0 else) and p_i , p_j , the relative abundance of species i and j in each sample. When d_{ij} is composed of 0 and 1 as in our case, Rao's quadratic entropy is equal to the Gini-Simpson diversity index and is related to the *true diversity* D (Jost, 2007; Tuomisto, 2010a) and the Jost's 'number equivalents' (Jost, 2007; de Bello *et al.*, 2010a):

$$\text{(a) } D_\gamma = \frac{1}{1-Q_\gamma}, \text{ (b) } D_\beta = \frac{1}{1-Q_\beta} \text{ and (c) } D_\alpha = \frac{1}{1-\overline{Q}_\alpha} \quad (2)$$

The true **β** diversity component D_β is 'the number of communities that have no diversity overlap' in de Bello *et al.* (2010a, p. 995) and Q_β represent 'the proportion of diversity accounted for by the differentiation between communities' (de Bello *et al.* 2010a, p. 996). In Tuomisto (2010a, p.12) Q_β corresponds to the 'proportional effective species turnover' (with an order of diversity $q=2$). The turnover formula is thus:

$$Q_\alpha = \frac{D_\gamma - D_\alpha}{D_\gamma} = \frac{Q_\gamma - \overline{Q}_\alpha}{1-\overline{Q}_\alpha} \quad (3)$$

where $\overline{Q}_\alpha$ is the mean quadratic entropy of the selected plots, and Q_γ is the quadratic entropy including all species from the selected plots. To

calculate Q_α, $p_i=p_j=1/S_x$ when the species is present (S_x is the species richness of the xth plot) and $p_i=p_j=0$ when the species is absent. To calculate Q_γ, p_i is the mean across all plots x of all p_{ix} (de Bello *et al.*, 2010a).

We measured the Rao beta diversity index using the 'disc' function in the 'ade4' R software package (Rao, 1982). The values were then multiplied by 100 and therefore range from 0 (no turnover) to 100 (complete turnover). A comparison with other indices is included in Appendix S1 in the Supporting Information. In our case the chosen index is very similar to the Jaccard index used in a similar study (Manthey et al., 2011), because there are neither abundance data nor distances between species (Pearson's product–moment correlation coefficient between the two indices = 0.9944, see Table S1 in Appendix S1).

In order to compare the observed values to the random expectations for theta distribution we performed a null model analysis that assumed there to be no niche constraint or dispersal limitation. We computed the turnover among 10 plots randomly selected in the dataset 999 times. This allowed us to estimate the potential range of theta across the study region, for the same number of sampling sites.

Species' niche breadth has often been seen as a species property related to species rarity (Rabinowitz *et al.*, 1986). Here we explored the relationship between the specialization index, which measures the ecological range of a species, and two facets of species rarity at regional and local spatial scales (Gaston, 1997). The regional rarity referred to each species' area of occupancy in the study region. This area was estimated by a convex hull, which is the smallest polygon containing all line segments between each pair of species occurrences. This method is relatively widely used in ecology to measure area (for a recent example, see Cornwell *et al.*, 2006). We used the function 'calcConvexHull' in the R package 'PBSmapping' (for the algorithm, see Eddy, 1977). This function computed the convex hull polygon from a set of points. The local rarity referred to local abundance. It was measured from the

average local relative abundance of a given species across all sample sites. This measurement therefore captures the mean dominance of each species within the communities where it occurs (Kunin & Gaston, 1993; Kunin, 1997). To describe the relationship between the specialization and the two rarity measurements, we used generalized least squares regressions that account for heterogeneous variance in the residuals (Durbin–Watson test for homogeneity rejected: *P*-values < 0.01). We used the function 'gls' in the R package 'nlme', with the variance increasing or decreasing as a power of the absolute fitted values. The proportion of variance explained was estimated by the adjusted R^2 *of* the regression between observed and predicted theta values.

All comparisons between plant specialization and ecological characteristics (life span, Raunkiaer life-forms and Grime strategies) were made using Fisher tests or the Kruskal–Wallis nonparametric test of means when variances were too heterogeneous between groups. All statistical analyses were carried out using R 2.11 software (R Development Core Team, 2010).

RESULTS

Overall patterns of species specialization

(a) (b)

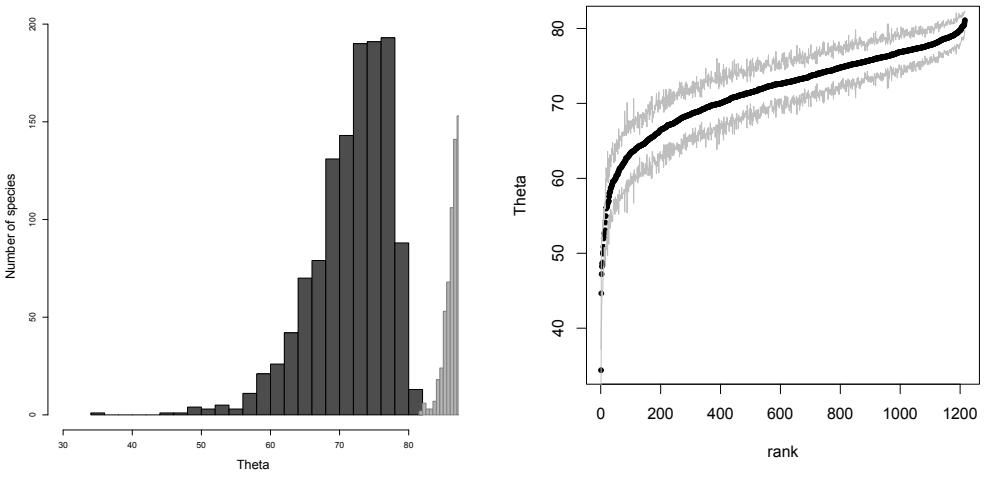

Figure I.2 Specialization index distribution for 1216 French alpine plants. (a) Distribution of the specialization index and its associated null model. The specialization index theta ranges from 0 (specialist) to 100 (generalist). The light grey histogram represents 999 random turnover of species across 10 plots of the area studied. The dark grey histogram contains the mean observed values for 10 plots containing each focal species. All the random values are above the mean observed values by species. (b) Specialization index and standard error around the estimator. The black dots indicate the specialization index (theta*)*. Two grey lines are plotted at theta +/- standard deviation. Species are ranked according to their specialization index.

The 1216 species analysed showed a skewed distribution of theta ranging between 35 and 80. For all species, the specialization index was lower than random expectation (ranging from 81 to 90, Fig. 2a), which

implies strong niche differentiation in the plant communities investigated (plant species did not co-occur randomly). This comparison to the null model ensured that the ecological range of the study area is large enough to capture the ecological limits of most study species. The average standard deviation per species was 2.9 (6% of the total range of theta for all species in the study). This standard deviation was negatively correlated with the theta estimate (see Fig. 2b), indicating that generalist species tend to yield theta estimates with lower standard deviation. This relationship has already been observed and seems to be inherent to the method (see Fridley *et al.*, 2007). We were able to draw out a group of super-specialist species with theta values under 60. These species were found in various habitats, but most of them preferentially occurred in wetland, dry scrublands or alpine habitats (Fig. 3). The three most specialist were typical peat bog species (*Scheuchzeria palustris, Carex limosa* and *Drosera rotundifolia*). Other highly specialized species were alpine marsh species (*Carex maritima* and *Carex microglochin*) and alpine grassland species from windy crests (*Minuartia recurva*) or late melting snow-beds (*Pedicularis ascendens*). Species associated with dry Mediterranean scrublands were also highly specialized (*Ruta angustifolia, Rosmarinus officinalis, Fumana thymifolia, Coris monspeliensis, Lonicera implexa* and *Globularia alypum*). Only one scree species (*Viola cenisia*) was found among the highly specialized species. Finally, some specialists were associated with human disturbed habitats (*Setaria pumila, Digitaria sanguinalis, Panicum capillare* and *Setaria viridis*).

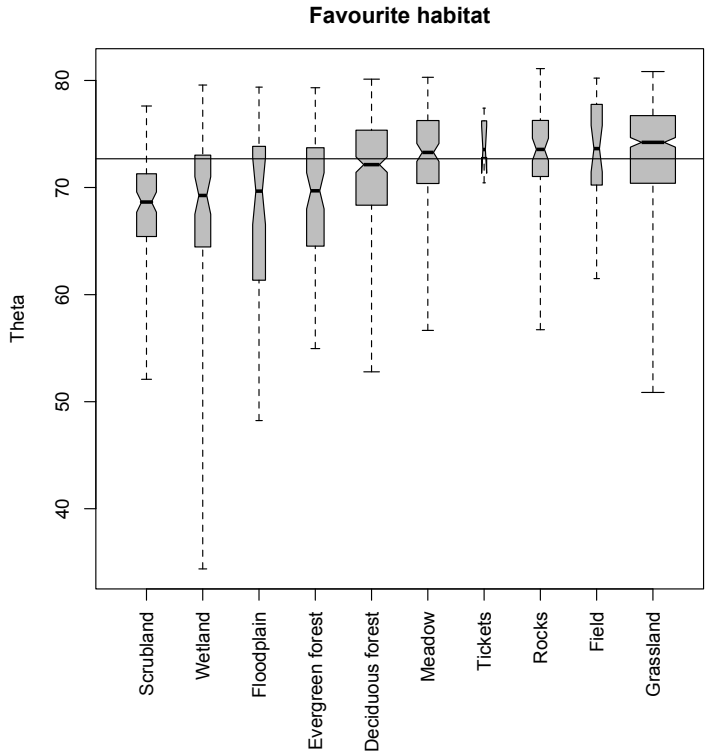

Figure I.3 Specialization index among 1216 French alpine plants grouped according to their favourite habitats. Box plots show extremes values and quartiles. The horizontal line indicates the median theta for all species. The black dots represent the most specialized species. Widths are proportional to the square root of the number of species in each class. If the notches for two plots do not overlap then the medians are significantly different at $\alpha = 0.05$. The theta index ranges from 0 (specialist) to 100 (generalist). The means for each group are significantly different (Kruskal–Wallis rank sum test: P-value < 2.2×10^{-16}).

Specialization and rarity

(a) (b)

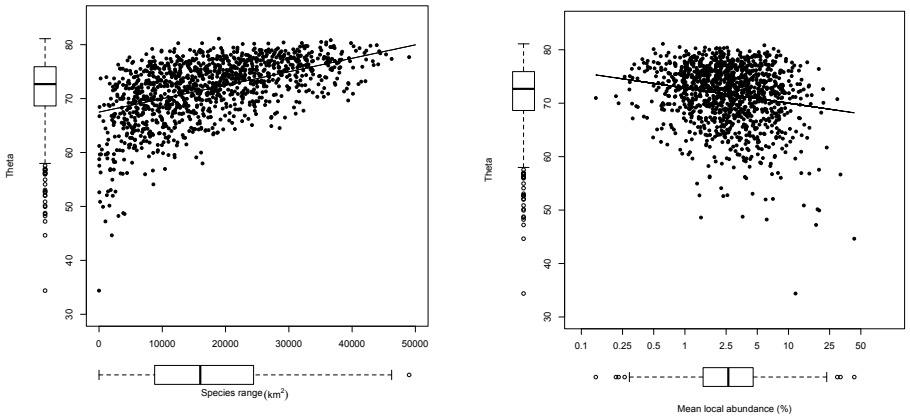

Figure I.4 Specialization index of 1216 French alpine plants as a function of two different measures of rarity. Box plots along each axis show extreme values and quartiles. The middle line indicates the median value for all species. (a) Specialization as a function of the regional area of occupancy (km^2). The solid lines indicate the generalized least squares regression fit. The slope is significantly different from zero (P-value < 2×10^{-16}). Adjusted R^2 = 30.3%. (b) Specialization as a function of the logarithm of the mean relative abundance in the community plots where the species occurs. The solid lines indicate the generalized least squares regression fit. The x-axis is log-scaled. The slope is significantly different from zero (P-value < 2.2×10^{-16}). Adjusted R^2 = 4.5%.

The specialization index was correlated with our two rarity measures. The comparison between specialization and species geographical ranges showed a positive trend, indicating that generalist species are usually widespread species whilst specialist species tend to be geographically restricted (Fig. 4a). The generalized least squares regression slope was significantly different from zero (P-value < 0.001) and the variance explained was meaningful (adjusted R^2 = 30.3%). However, some generalist species were detected even among species with narrow

geographical ranges, suggesting that high theta is not a mere by-product of the species' regional area of occupancy. Conversely the local abundance was negatively correlated with the specialization index (Fig. 4b) implying that specialist species (low theta) are more often dominant in their communities than generalist species (high theta). The linear regression slope was significantly different from zero (P-value < 0.001) while the model's goodness of fit was relatively low but still significant (adjusted R^2= 4.5%).

Ecological characteristics and plant specialization

There was no significant relationship between species life span and species specialization, nor was there any significant difference in terms of specialization between the three broad life history classes (Kruskal–Wallis rank sum test: P-value = 0.1238). However, the group of highly specialist species appeared in herbaceous classes only.

There were significant differences in species specialization between Raunkiaer life forms (Kruskal–Wallis rank sum test: P-value = 0.02934, Fig. 5a). Therophyte species were mainly generalists, while helophytes, phanerophytes and geophytes were generally specialists.

As expected, there was a significant relationship between species specialization and their Grime classification (Kruskal–Wallis rank sum test: P-value = 3.766×10^{-5}, Fig. 5b). Stress-tolerant and stress-tolerant competitor species (S and CS) were more specialized. Pure competitors (C) were mostly generalists. There was no difference in the degree of specialization for ruderal and ruderal competitor species (R and CR) and for species with mixed strategies (CSR) in comparison with the mean specialization.

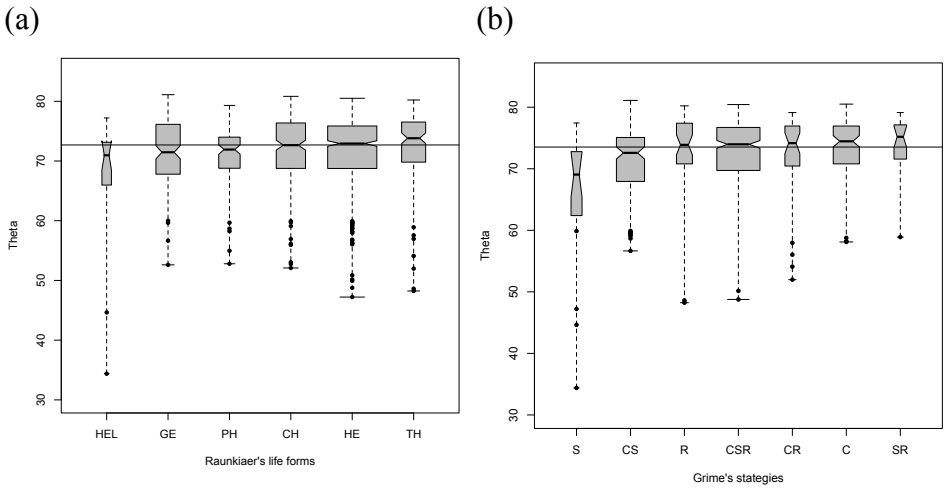

Figure I.5 Specialization index among 1216 French alpine plants grouped according to their traits. Box plots show extreme values and quartiles. The horizontal line indicates the median theta for all species. The black dots represent the most specialist species. Widths are proportional to the square root of number of species in each class. If the notches for two plots do not overlap then the medians are significantly different at $\alpha = 0.05$. Theta index ranges from 0 (specialist) to 100 (generalist). (a) Specialization index among Raunkiaer's life forms. CH=chamaephytes; GE=geophytes; HE=hemicryptophytes; HEL=helophytes; PH=phanerophytes; TH=therophytes. The means for each group are significantly different (Kruskal–Wallis rank sum test: *P*-value = 0.02934). (b) Specialization index among Grime's strategies, for herbaceous species only. S = stress-tolerator, C = competitor, R = ruderal. The means for each group are significantly different (Kruskal–Wallis rank sum test: *P*-value = 3.766×10^{-5}).

DISCUSSION

In this paper we aimed to use an extensive vegetation survey across the French Alps region, that encompasses a wide elevational gradient, to investigate the overall pattern of plant specialization. With regard to our first objective, we have indeed shown that specialized species tend to be found in specific habitats located on the edges of environmental gradients, namely xeric Mediterranean scrublands, wetlands, or alpine grasslands. We have also demonstrated that specialist species appear to be over-represented in the hydrophyte and geophyte life form classes, and are mainly associated with Grime's stress-tolerant strategy. Our analysis shows that habitat specialization positively correlates with a species' area of occupancy, and to a lesser extent inversely correlates with the species' local dominance.

An integrated index of specialization

The unbiased measurement of species specialization in a large species sample has always seemed problematic. The approach we use was shown by Fridley *et al*. (2007) to be unbiased with respect to the number of occurrences for each species (Fridley *et al.*, 2007). The same applies to our study, where the correlation between the specialization index and the frequency of occurrence is weak (adjusted $R^2 = 4.6\%$, see Appendix S2) whilst the variance of this frequency of occurrence within the dataset increases with increasing species' theta, which means that

there are no specialist species with a high number of occurrences in the dataset (Appendix S2).

More generally, the use of an integrated index of specialization is appealing as it is intended to include numerous species niche axes, as well as factors that may explain species coexistence on the local community scale. Fridley's theta framework is particularly interesting because of the re-sampling procedure that accounts for differences in species frequencies. Another advantage of this framework is that it is more flexible on the underlying distance measurements, for instance when compared to an indirect gradient analysis such as DCA. Although both approaches produce highly correlated results (Pearson correlation with theta = 0.7, see, Table S1 in Appendix S1), the DCA is based on a chi-square distance, which is not entirely comparable to turnover as measured by Rao, multiple Simpson or Jaccard indices.

A species-based niche breadth estimate is particularly useful in detecting local environmental effects, or niches axes that are only relevant for some species. For large-scale datasets, other methods based on species distributions and environmental data cannot include the local environment because this information is not usually documented in vegetation databases and it cannot be inferred from large-scale environmental data. Although high-resolution climatic data and land cover variables are increasingly available (Hijmans *et al.*, 2005), they are usually interpolated or modelled data with uncertainties inherent in the process and are therefore unable to capture local information or even landscape heterogeneity. We show that using a direct ordination method (outlying mean index, OMI) with six topographic and climatic variables results in a similar species ordination (Pearson's correlation with theta = 0.45, see Tables S1 and S2 in Appendix S1). This result is not entirely surprising because we preselected six variables that explain most of the environmental variation across the entire study area but probably fail to describe the local environmental conditions that explain species co-existence and species-specific requirements. By using species as indirect indicators of the environment we are able to take local conditions into account. With the same approach, Manthey *et al.*

(2011) suggest that some micro-environmental factors that are usually not taken into account may have led to overestimating the effect of competition between species. We also reveal the importance of the local environmental conditions defined by the vegetation structure. For instance, *Juncus subnodulosus* makes dense tussocks that may exclude other species in the community, creating a very specific habitat. Another example of the effect of vegetation structure is the impact of forest trees on the herbaceous plant undergrowth. In dark forests such as beech–fir (*Fagus–Abies*) forests we found a large proportion of specialist species, which could be explained by the effects of trees on herbaceous species (e.g. limiting light availability, retaining soil moisture). Furthermore, the canopy, which provides various resource-related stress levels, is known to change competitive relationships between species (Maestre *et al.*, 2009).

Which species are more likely to be specialized?

Theoretically, specialist species are confined to a small part of the ecological space where they can locally outcompete species belonging to the competitor strategy class, which are less adapted to a specific habitat (Wisheu, 1998). Our findings corroborate this hypothesis, as most specialist species are preferentially dominant in the communities where they occur (Fig. 4b). Specialist species are indeed mainly located in stressful habitats and co-occur with the few other species adapted to the extreme local conditions. Consequently, they tend to have high relative abundance. On the other hand, generalist species may be found in very rich communities where competition is intense, leading to high species evenness.

There is a positive correlation between the specialization index theta and the geographical range (P-value $< 2.2 \times 10^{-16}$, $R^2 = 30.3\%$). We did however observe that generalist species are not necessarily widespread because variance in the geographical range increases with increasing species' theta. This pattern could be explained by a high level of environmental heterogeneity across the region and the landscape mosaics, implying species experience a wide range of environmental

conditions over a restricted territory. Although species spreading across 20,000 square kilometres with a fairly low theta value have been observed, the more specialist the species are, the smaller their geographic range. This is certainly due to the main climatic gradients that are spatially auto-correlated (e.g. temperature). In this context, specialist species are more likely to be restricted to a small area due to their narrow tolerance of environmental conditions. However, some specific wetland specialized species, for instance, should be less sensitive to these gradients, implying relative independence between the geographical range and the ecological range. The observed spatial restriction of specialist species may relate to the effect of distance decay. As the species niche breadth is estimated from species co-occurrence, a wetland species may have high theta if it occurs in two distant sites that differ in species composition due to historical legacies and dispersal limitation.

In order to test whether some specialist species are hidden among generalists, we measured the number of distinct habitats used for every species, a commonly used measurement of niche breadth (Devictor *et al.*, 2010), and related it to theta. Although the habitats have been roughly defined, the two measures are consistent (Appendix S3, Kruskal–Wallis rank sum test: P-value $< 2.2 \times 10^{-16}$). In particular, species occurring in only one type of habitat have the lowest theta values. We therefore consider that theta is a satisfactory surrogate for estimating plant specialization for numerous species occurring in a wide range of habitats.

These two results challenge the established macroecological rule which stipulates that regional distribution and local abundance are positively related (Gaston & Lawton, 1990), by showing that this relationship does not hold (and indeed tends to be inversed) for specialist species (Fig. 4), which are located in habitats that turn out to be peculiar on the regional scale. However, it is difficult to generalize such patterns because they are sensitive to the study scale and to the measures of regional and local abundances that are used.

Longevity attributes do not distinguish generalists from specialists. Nevertheless, specialist species are not randomly distributed across life-form classes. Therophytes are over-represented amongst generalist species, which may be explained by the fact that they are opportunistic and pioneering annual plants capable of colonizing bare ground after a disturbance, which could occur in very different habitats. However, some of these species may occur in very specific habitats with sandy or acid soils. Conversely, helophytes are disproportionately represented amongst specialist species, which may be due to the particular adaptations required by wetland habitats. The geophytes class also contains numerous specialist species, which could be explained by the fact that they invest resources in bulbs or rootstock, which allows them to resist dryness or grazing (Hadar *et al.*, 1999; Jutila, 1999; Noy-Meir & Oron, 2001). This resistance mechanism implies a trade-off that limits the potential of species to adapt to a large range of habitats.

The comparison of the specialization index to Grime's strategies corresponded to expected trends. Pure competitors are overrepresented among generalists whereas species classified as stress-tolerant tend to be specialists. Once again this may be viewed as an empirical validation of the tolerance–dominance trade-off (Wisheu, 1998). Species that are generally weak competitors may have found refuge and adapt at the extreme end of environmental gradients, where generalist species may fail to become dominant. On the other hand, competitive lotteries may allow pure competitors to become locally dominant over a wider range of habitats within the limits of their physiological tolerances, thus making them appear to be more generalist species.

Conclusions

In this paper we estimate niche specialization for a large number of plant species using an approach that makes it possible to account indirectly account for various factors that either explain species coexistence on both regional and local community scale, or are only relevant for some specific species. Our results are an empirical validation of the tolerance–dominant trade-off, showing that specialist

species are not strong competitors (*sensu* Grime's strategies), and generally find refuge on the stressful edges of environmental gradients, in communities where they tend to dominate.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

APPENDIX S1 SENSITIVITY ANALYSES USING SEVERAL BETA DIVERSITY MEASURES BETWEEN PLOTS AND TWO ORDINATION TECHNIQUES.

	Rao (de Bello *et al.*, 2010a)	Multiple Simpson (Baselga *et al.*, 2007)	Multiple Sørensen (Baselga *et al.*, 2007)	Jaccard	Multiplicative beta (Whittaker, 1960)	Additive beta (Lande, 1996)	Indirect ordination (DCA) (ter Braak, 1988)	Direct ordination (OMI) (Dolédec *et al.*, 2000)
Rao	1.0000	0.9541	0.9321	0.9944	0.9278	0.7718	0.7178	0.4544
Multiple Simpson	-	1.0000	0.9459	0.9679	0.9419	0.7772	0.7231	0.4916
Multiple Sørensen	-	-	1.0000	0.9557	0.9960	0.6275	0.7351	0.4522
Jaccard	-	-	-	1.0000	0.9516	0.7577	0.7214	0.4563
Multiplicative beta	-	-	-	-	1.0000	0.6273	0.7339	0.4520
Additive beta	-	-	-	-	-	1.0000	0.4640	0.4095
Indirect ordination	-	-	-	-	-	-	1.0000	0.3095

We computed the specialization index using five other measures of beta diversity included in Manthey & Fridley (2009): the original measure named 'additive beta', the Jaccard index, two other indices based on either Simpson or Sørensen index for multiple sites (see Baselga, 2009) and one based on R.H. Whittaker's decomposition called 'multiplicative beta'. The index chosen for our study is based on Rao's quadratic entropy formula as in de Bello *et al.* (2010a). The comparison between indices showed little variation. Only the originally proposed index, the additive beta, really differed from the others (Table S1).

We also estimated species specialization using both indirect and direct species ordinations. For the indirect ordination, we chose a detrended correspondence analysis (DCA) because our dataset was large and

heterogeneous. For the direct ordination, we used six variables (moisture index for the growing season, mean daily monthly mean temperature, winter precipitations, potential yearly global radiation, slope and topography) and we ran three analyses: canonical correspondence analysis (CCA) and redundancy analysis (RDA) (ter Braak, 1986, 1988) and outlying mean index (OMI, Dolédec *et al.*, 2000). Given that OMI explained significantly more inertia than CCA and RDA (76% for OMI, 55% for RDA and 47% for CCA), we only calculated niche specialization over the first axis of the OMI. The direct ordination differs the most from other niche breadth estimations. The DCA is similar to theta estimates except for additive beta (Table S1).

Sensitivity analysis: varying the number of plots randomly sampled to compute beta diversity.

The choice of this parameter is arbitrary. However, it determines the potential number of species to be included in the study. The species that have been recorded under the chosen value were not excluded from the community plots, but their *theta* values were not calculated. We compared the specialization index computed using three different values for this parameter (5, 10, 15) and only for species that have been recorded more than 20 times in our dataset in order to be able to estimate standard deviation for each species. The comparison showed the analysis had very limited sensitivity to this parameter (Table S2).

Number of plots	5	10	15
5	1.0000	0.9943	0.9945
10	-	1.0000	0.9979

Table I.S2 Correlation matrix (Pearson product–moment correlation coefficients) between three specialization measures for 1216 French alpine plants, using different values for the number of plots used to compute beta diversity.

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APPENDIX S2

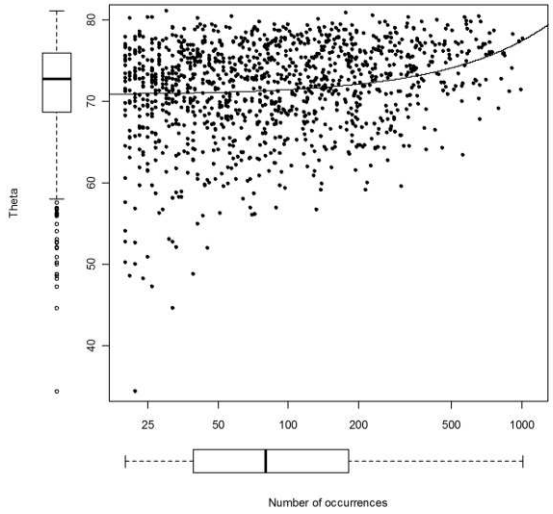

Fig. I.S2 Specialization index for 1216 French alpine plants according to the number of occurrences in the dataset. The solid grey line indicates the generalized least square regression fit. The *x*-axis is log-scaled. The slope is significantly different from zero (*P*-value <0.001). Adjusted R^2 = 4.6%. The boxes on the axes represent the distribution of the variables for each axis.

APPENDIX S3

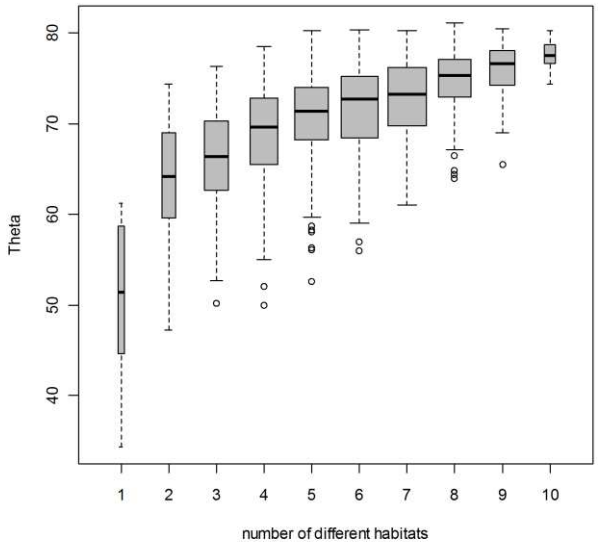

Fig. I.S3 Specialization index for 1216 French alpine plants, according to the number of habitats in which a species occurs in the dataset. The ten habitat classes are the same as those used in the rest of the study. Box plots show quartiles. Widths are proportional to the square root of number of species in each class. Theta index ranges from 0 (specialist) to 100 (generalist). The difference between mean theta values across the number of habitats is significant (Kruskal–Wallis rank sum test: *P*-value < 2.2×10^{-16}). Very generalist species (high theta) are species occurring in numerous habitats, whereas very specialist species occur in few habitats.

CHAPITRE II:

ACCOUNTING FOR DISPERSAL AND BIOTIC INTERACTIONS IN ORDER TO DISENTANGLE THE DRIVERS OF SPECIES DISTRIBUTIONS AND THEIR ABUNDANCES

Boulangeat, I., Gravel, D. and Thuiller, W. (2012) Accounting for dispersal and biotic interactions in order to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, **15**, 584-593.

Statement of authorship**:** WT, DG and IB designed the study. IB performed the analyses and led the writing. All the authors contributed substantially to the writing.

Editor David Storch

Abstract

Although abiotic factors, together with dispersal and biotic interactions, are often suggested to explain the distribution of species and their abundances, species distribution models usually focus on abiotic factors only. We propose an integrative framework linking ecological theory, empirical data and statistical models to understand the distribution of species and their abundances together with the underlying community assembly dynamics. We illustrate our approach with 21 plant species in the French Alps. We show that a spatially nested modelling framework significantly improves the model's performance and that the spatial variations of species presence-absence and abundances are predominantly explained by different factors. We also show that incorporating abiotic, dispersal and biotic factors into the same model bring new insights to our understanding of community assembly. This approach, at the crossroads between community ecology and biogeography, is a promising avenue for a better understanding of species co-existence and biodiversity distribution.

INTRODUCTION

Understanding the factors driving the distribution of species and their abundances is an important research area in ecology since it refers to species coexistence and the maintenance of species diversity (Chesson 2000a). Soberon (2007) proposed a conceptual framework distinguishing three main drivers. Abiotic constraints delimit the species' fundamental niche within which the species could establish and maintain itself given its intrinsic physiological limits (Chase & Leibold 2003). Dispersal limitations may then restrict a species' range by preventing it from reaching a suitable site. Dispersal limitation is inherently linked to the species' dispersal capability, but may also be influenced by historical legacies (Vellend *et al.* 2007). Some species may reach high abundance in unsuitable sites due to frequent immigration from neighbouring suitable sites, as predicted by source-sink dynamics or mass effect (Pulliam 2000). Finally, biotic interactions may modify either the resources availability or the local abiotic environment with potentially contrasting consequences on abundance (e.g. competition and facilitation, Lortie *et al.* 2004). These three main drivers could interact together and influence the observed spatial distribution of the environmental conditions suitable for a given species (i.e. species' realized niche).

These drivers of species distributions may act at different spatial scales (Kneitel & Chase 2004). For instance, frequent consideration is given to abiotic variables acting at large spatial scales (Davies *et al.* 2004). Climate and soil variables have been shown to be the most relevant variables when predicting continental to regional-scale plant species presence-absence distributions (Thuiller *et al.* 2004b). Other factors, such as land cover, are also important to understand species distribution at regional scales (Randin *et al.* 2009b). On the other hand, biotic interactions and consumer-resource dynamics are assumed to occur at smaller spatial scales (Soberon 2007). Dispersal limitations are most likely to occur at a larger extent than species dispersal distances, whereas source-sink dynamics occur at the same scale as dispersal.

So far, species distribution has been modelled using species distribution models (SDMs), which, most of the time, ignore the effects of dispersal and biotic interactions (VanDerWal *et al.* 2009). Even if SDMs provide satisfactory predictions for presence-absence, they typically fail to explain and predict species' abundances across sites (Pearce & Ferrier 2001; Sagarin *et al.* 2006). Here we argue that this failure is due to the omission of the above-mentioned dynamic drivers (i.e. dispersal, biotic interactions) and that all processes acting at different spatial scales are fitted in a unique response model. The abundance of a given species is obviously driven to some extent by the same processes as the presence-absence, but additional processes might come into play to determine the abundance when the species is present. They operate at finer resolutions where community composition, population dynamics and the microenvironment interact. For explaining and modelling species abundances, the use of a spatially nested approach, which model separately the processes underlying presence-absence and abundance variation, seems therefore particularly relevant.

We propose to account explicitly for the spatial nestedness of processes in a comprehensive modelling framework where the species undergoes successive filters. The first filter, related to larger scale factors, determines the presence or absence of the species. This filter is expected to be primarily driven by abiotic variables (eco-physiological limitations) and by dispersal when site accessibility is limited. Once a species is able to reach a suitable site, the second filter, expected to be mainly determined by local scale factors such as biotic interactions and dispersal in case source-sink dynamics occur, will determine the local abundance and other absences (Fig. II.1, Theoretical model). Our objective here is to test these expectations using an operational statistical framework (Fig. II.1, Model structure). Firstly, we introduce a set of key innovations to account for biotic interactions, using co-occurrence based indices, and for dispersal by proposing a measurement based on species dispersal capabilities and observed spatial distributions. Secondly, in order to separate presence-absence from abundance underlying processes, we propose a two-step modelling approach: (1) modelling species presence

and absence, and (2) modelling abundances once presence has been determined. We highlight the innovative nature and outputs of our framework with the modelling of 21 plant species in the French Alps. We show how our framework separates the drivers of presence-absence and abundances. We then demonstrate how consideration of biotic interactions and dispersal not only improves predictions of species distributions, but also provides better knowledge of the elusive fundamental niche and explores the key drivers of abundances within their niches.

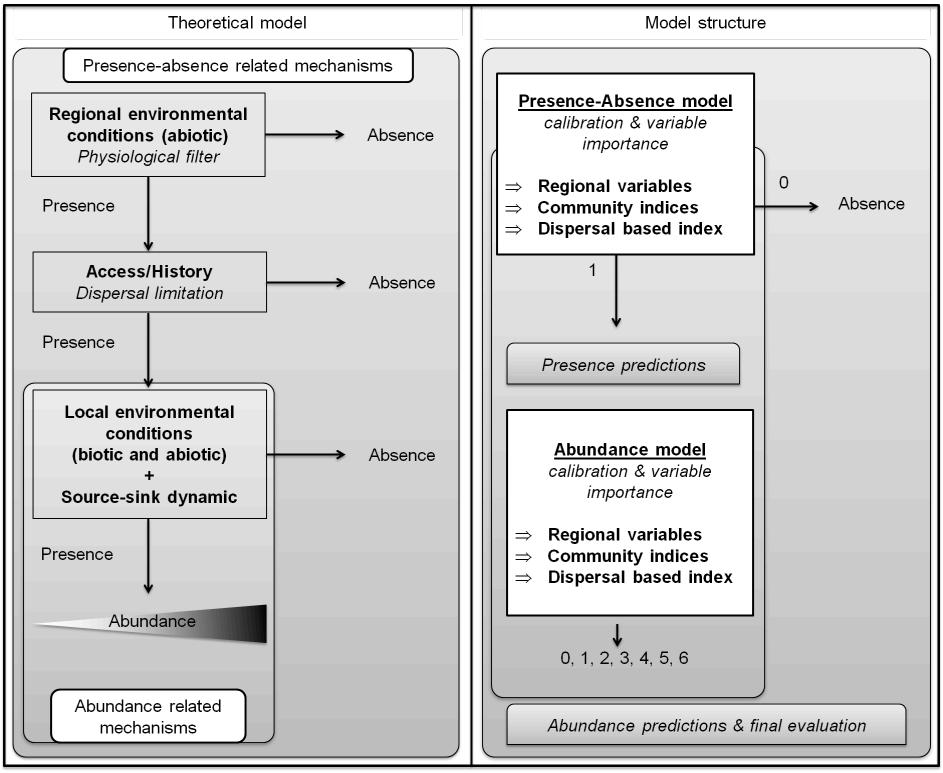

Fig. II.1 Theoretical framework and model structure. The aim of the nested model structure is to represent the theoretical framework. The first model focuses on presence-absence only and is expected to primarily involve abiotic drivers due to physiological filtering and dispersal mechanisms due to dispersal limitation. The second model focuses on abundance when presence has been assessed and is expected to involve local-scale mechanisms, including abiotic and biotic community-scale effects and source-sink dynamics.

MATERIALS AND METHODS

We applied our framework independently to 21 plant species representative of the French Alps. We selected species with a reasonable number of observations in different abundance classes and represent varying life forms and dispersal abilities (Supporting Information Tabs II.S1 and II.S2). The idea was to test our framework and underlying hypotheses with a set of species that were sufficiently different to permit robust conclusions. Sampling spread over a region of 30,000km^2, from lowlands to alpine summits (Supporting Information Fig. II.S1).

Vegetation database

We used a database of vegetation surveys provided by the National Alpine Botanical Conservatory (CBNA), including 8,160 community-plots sampled in natural or semi-natural areas from 1980 to 2009 (Fig. II.S1 left) and with a total of 2,170 plant species (Boulangeat *et al.* 2012). Plot size information was not systematically available but was approximately 10x10m. Within each community-plot, species abundances were recorded using a cover scheme with six classes (1: less than 1%; 2: from 1 to 5%; 3: from 5 to 25%; 4: from 25 to 50%; 5: from 50 to 75%; 6: up to 75%) (Braun-Blanquet 1946). Species abundance classes were converted to relative abundances for co-occurrence based indices (see below). We first converted cover classes to their mean percentages (0.5%, 3%, 15%, 37.5%, 62.5%, 87.5%) and then normalized them between 0 and 1 to obtain the relative abundance of each species.

We used a second dataset from the same source (CBNA) to build the dispersal-based index and some of the co-occurrence based indices (see below). This dataset contains approximately two million spatially localized single occurrences (i.e. presence-only data, Fig. II.S1 right) recorded from 1980 to 2009. Each of the 2,170 plant species has been recorded at least 20 times.

Abiotic variables

We considered climate, topography and soil (see Supporting Information Tab. II.S3 and Fig. II.S2). Four climatic variables (temperature, precipitation, moisture index and radiation) were extracted from the Aurelhy meteorological model (Bénichou and Le Breton, 1987), based on interpolated measurements at a resolution of 100x100m. We used a 50x50m digital elevation model to generate slope angle (°), topography (elevation range within the pixels) and the topographic wetness index. Soil carbon and available water capacity were extracted from the European soil database (1x1 km). We used land cover maps (100mx100m) extracted from the 2006 Europe-wide Corine Land Cover (artificial surfaces, agricultural areas, forest, scrub, open spaces, wetlands

and water bodies) (see Tab. II.S3) to build the dispersal index and the expected community assembly (see below). For community plots, we assigned a land cover type from the plot description provided by the botanists (i.e. wetland, open land, shrubland and wood), pairing the European Corine land cover classification (Bossard *et al.* 2000).

Dispersal based index

We developed an index modelling the potential effects of dispersal on species distribution and abundance. It aimed to account explicitly for the spatial auto-correlation of species distributions with the inclusion of the biological hypotheses underlying species dispersal abilities. This index was based on a seed rain model and the integration of the species presence-absence distribution in the neighbourhood of the community (Fig. II.2).

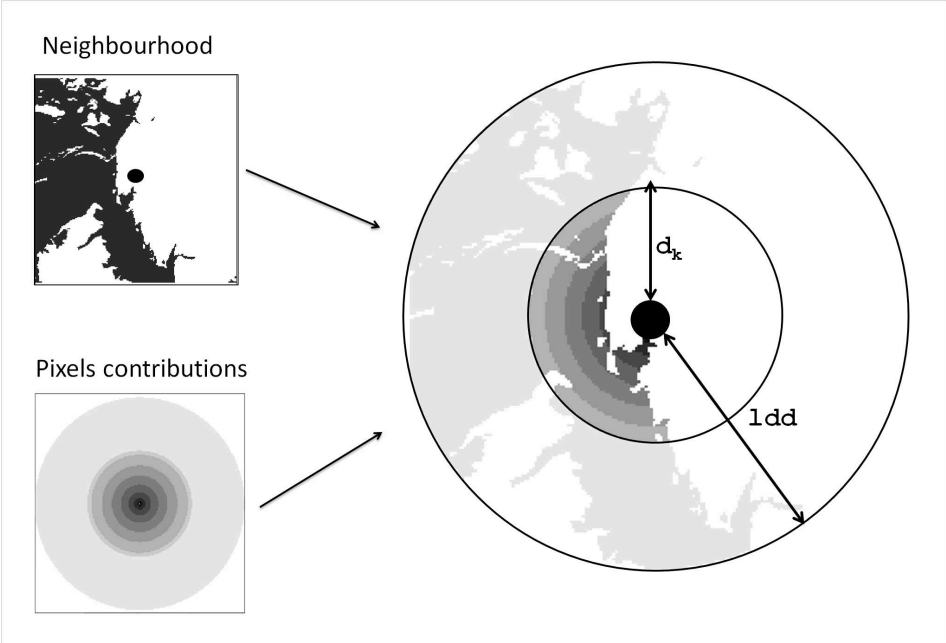

Fig. II.2 Contribution of neighbouring cells to the dispersal-based index. A kernel function is applied to weight species presences around each focal cell (sampled point, black dot). Pixels under distance d_{99} contribute by short distance dispersal and pixels between d_{99} and ldd contribute by long distance dispersal (see equations). The neighbourhood map displays the species presence (black) and absence (white) around the focal community. The pixel contribution map shows the weights of each pixel. The resulting map is then added up to obtain the potential seed rain, known as the dispersal-based index.

We first approximated the actual spatial patterns of species presences and absences at the regional scale using traditional SDMs because a complete sampling of the entire region at a reasonable resolution is practically impossible. We assumed that there would be a strong match between the first environmental filter and the presence-absence distribution at a coarse resolution (100x100m). We used random forest models as they have been shown to be of very good predictive accuracy (Peters *et al.* 2007). Our objective was to closely match the observed distribution and

only detect potential missing presences (not sampled). The calibrations were made using all available species observations (i.e. using both datasets, with a minimum of 500 presences per focal species) and all gridded abiotic variables (Fig. II.S2).

Based on these estimated presence-absence distributions (Supporting Information Fig. II.S4), we modelled the potential seed rain received each year in a plot using a spatially-explicit dispersal model (adapted from Engler *et al.* 2009). The expected seed rain of a species in a plot was modelled as an integration of the presences in the neighbourhood weighted by a species-specific seed dispersal kernel. The neighbouring pixels (from 0m to a threshold distance d_k) contributed to the seed rain as:

(Eq.II.1)
$$\frac{\exp\left((r-R).\frac{\ln(1-k)}{d_k}\right). - \exp\left(r.\frac{\ln(1-k)}{d_k}\right)}{\frac{2.\pi.r}{R}}$$

where r is the distance from the pixel to the community, k is the proportion of seeds that fall before the distance dk and R is the pixel size (here 100m). The long distance pixels, from distance dk to maximal dispersal distance ldd, contributed to the seed rain as:

(Eq.II.2)
$$\frac{1-k}{\pi.(ldd+d_k).(ldd-d_k)}$$

The parameter k was fixed at 0.99, and ldd and d_{99} were assigned from independent literature information in accordance with Vittoz & Engler (2007) and Engler *et al.* (2009) (Supporting Information Tab. II.S2). The species-specific dispersal index for a site was the overall potential seed rain received in a community-plot (Eq. II.1 + Eq. II.2) integrated over all neighbouring pixels (Fig.II.2). Despite the effect of the abiotic environment on species distributions and thus on the dispersal index, the correlations between dispersal index and abiotic variables were lower

than 0.7 for the 21 focal species and all variables (Supporting Information Tab. II.S4).

Co-occurrence based indices

We computed four site-specific co-occurrence-based indices to estimate the effects of biotic interactions on species distribution. The indices aggregated pair-wise species interaction strength measurements at community level. We took into account the interactions between each of our 21 species with all species occurring in the French Alps dataset. We used three different strategies based on (1) the observed co-occurrences, (2) the expected community composition according to abiotic environmental filters, and (3) a comparison between observations and expectations. The rationale was to depict resource competition and coexistence resulting from species interactions. Observed species co-occurrences (1) were a proxy for actual species interactions. Expected species co-occurrences (2) described the potential competitive pressure. The comparison between the two (3) measured the resulting species interactions when controlling for the effect of the abiotic environment.

1) Observed co-occurrences (Community Aggregated C-score).

Pair-wise species association strengths between the focal species *j* and the co-occurring species *k* were calculated using the C-score measure (Stone & Roberts 1990). Pair-wise C-score represents the average number of checkerboard units (i.e. when the two species occur in distinct sites) and was calculated as $(N_j-N_{jk}).(N_k-N_{jk})$, were N_j and N_k are the regional number of observations of species *j* and *k* respectively, and N_{ik} the number of co-occurrences between *j* and *k*. Pair-wise C-scores were then aggregated at the community level, weighted by the relative abundance of species *k* (p_k).

(Eq.II.3) $$I_{jx} = \sum_k I_{jk} . p_k$$

where I_{jk} was the pair-wise C-score between the focal species *j* and another species *k* and I_{jx} the community aggregated C-score at site *x*. A

value close to zero indicates independence between the focal species and the local community. Conversely, a high value suggests a strong repulsion between the focal species and the local community.

2) Expected co-occurrences (niche overlap index).

Expected communities (i.e. expected species co-occurrences) were constructed by relating observations to abiotic variables for all species involved in the sampled communities (2,170 species). A species was expected to be present in a community-plot if the local conditions fell into the observed species' environmental range, delimited by minimum and maximum observed values for all abiotic variables simultaneously. The rationale behind this was to identify those species that were not observed in locations potentially suitable for them. Species found in the community-plots could be viewed as the 'winners' that had already withstood the prevailing biotic interactions within their communities. By accounting for all species for which the environment of the observed community-plots were suitable, we took into account the 'absent' part of biodiversity or 'dark diversity' that theoretically could inhabit a particular site after accounting for the physiological constraints (Pärtel *et al.* 2011).

The niche overlap index was evaluated in each plot by accounting for all species expected to be present in the site and their niche overlap with the focal species. The abiotic niche space was defined by the first two axes of a principal component analysis (PCA, the first two axes accounted for 73% of the total variation) of all pixels of the study region (at a resolution of 100mx100m) and all abiotic variables. Species niche overlaps were calculated in the abiotic space using the D statistic (Schoener 1968). It ranges from zero to one (method adapted from Broennimann *et al.* 2011). The niche overlap index was calculated as the mean D between all species expected to be present in a given site and the focal species. It aims at describing the competitive pressure of the expected species pool on the focal species.

3) Observed and expected co-occurrence comparison (attraction and repulsion indices).

We derived two indices based on a comparison between the observed and expected species co-occurrences. The rationale for this comparison was to partition the effect of positive vs. negative biotic interactions (or other local factors). Both indices (for repulsion and attraction) were estimated by comparing the two community matrices (observed and expected, Tab. II.1). Negative co-distribution (fewer co-occurrences than expected, repulsion) should occur if species compete intensively with each other (Tab. II.1). Positive co-distribution (higher co-occurrences than expected, attraction) should occur if they positively interact with each other, or alternatively the presence of one species changes the local environmental conditions in such a way that a suitable habitat is created for the non-expected species (Gilpin & Diamond 1982). Two types of pair-wise interactions were calculated in order to quantify repulsion, (I_{jk} = (C_{01}+C_{10}) / (C_{01}+C_{10}+C_N+C_0)) or attraction (I_{jk} = (F_{01}+F_{10}) / (F_{01}+F_{10}+F_N+F_0)) (Tab. II.1) and aggregated at the community level (from Eq.3). Resulting indices quantified total negative (repulsion) or positive (attraction) interaction between the community and the focal species.

Table 1. Classification of the different cases arising from the comparison between expected and observed co-occurrences. Comparison of the observed (realized) co-occurrences with the expected ones (potential) for each species pair. Situation 1: both species are expected (1/1). If one species is not observed (C_{10} or C_{01}), it is the consequence of competitive exclusion or of an unsuitable local environment. Other configurations are neutral (C_N) or are the result of unconsidered factors (C_0). Situation 2: only one species is expected (1/0 or 0/1). If both species are observed (F_{01} or F_{10}), it is the consequence of a facilitation effect or a common local suitable environment. Other situations are neutral (F_N) or are the result of unconsidered factors (F_0).

Expected co-occurrence	Observed co-occurrence	Interpretation	Name
1/1	1/0	Competition or specific environment	C_{10}
	0/1		C_{01}
	1/1	Neutral	C_N
	0/0	Other factors	C_0
1/0	1/1	Facilitation	F_{10}
0/1			F_{01}
1/0	1/0	Neutral	F_N
0/1	0/1		
1/0	0/1	Other factors	F_0
0/1	1/0		
1/0	0/0		
0/1			

Species abundance model

We followed the nested modelling framework presented in the Introduction (Fig.II.1). Inspired by the general idea of Zero Inflated Poisson models for count data (Welsh et al. 1996), we first modelled species presence and absence and then, in a second step, we did the same with abundance cover classes for locations with predicted presence. In order to evaluate the models, final predictions were given by absences predicted from the first model and abundance classes (potentially including other absences) predicted using the second model (see Supporting Information Fig.II.S3 for a detailed workflow of the method). We compared this nested model to a non-nested model (i.e. without the first step) in order to evaluate its performance.

We used random forests (RF) to model both presence-absence and abundance data. This choice was driven by the ability of RF to deal with both binary and multilevel data and to estimate the importance of predictor variables in high dimensional settings. They provide estimates of the independent contribution of each predictor (Strobl et al. 2009). We performed nine repetitions, following a cross-validation procedure (see Fig. II.S3).

We calibrated and evaluated four models using different sets of predictor variables to evaluate the performance of our framework and estimate the relevance of the proposed indices: abiotic variables (A), abiotic variables and co-occurrence based indices (AC), abiotic variables and dispersal index (AD) and all predictors (ACD). Predictions about final abundance classes were evaluated using the Hanssen-Kuipers discriminant statistic (Gandin & Murphy 1992) (see Supporting Information Eq. II.S1 for the formula). We computed variable importance with a re-sampling method implemented into random forest models (Breiman et al. 2011) (see Supporting Information Eq. II.S2 for details and formula). We averaged the importance values across the nine repetitions and then normalized the results for each species by calculating the relative importance of the different variables. A variable was considered as not significant when the confidence interval included zero.

All analyses were carried out in R (R Development Core Team 2010) with the '*raster'* package for spatial data management, the 'ade4' package for PCAs, and the '*party'* package for random forest models and variable importance.

Biotic interactions and dispersal effects on the abiotic niche

We illustrated how community-scale and dispersal mechanisms affected the abiotic niche for the four species for which the addition of the proposed indices increased performance the most. We derived different predictions from the complete model (ACD) and projected them onto the abiotic niche space. This space was defined by the first two axes of a PCA involving the abiotic variables of the sampled plots. These two axes together explained 53% of the total inertia. In this space, we drew the density of presences derived from different model predictions, computed with observed values of explicative variables or with dispersal and/or biotic interactions set to zero. We grouped all repetitions into a single prediction. First, absences were determined where predicted absences had a majority amongst repetitions and then for presences, abundance classes were given by the majority amongst repetitions' predicted classes. Following Soberon (2007) we defined sinks as the sites where the model predicted presences with observed values but absences with null dispersal and we defined sources as the sites where the model predicted presences with observed values as with null dispersal. Then, in order to locate competition and facilitation areas, we compared the current predictions with predictions where all co-occurrence indices were set to zero. A predicted absence that became a presence with a release of biotic interactions indicated a negative impact of biotic interactions and conversely, a presence changed to absence indicated a positive impact of biotic interactions. We also compared the two response curves (current predictions and those with co-occurrence indices equalling zero) as a function of the temperature, which is the most important climatic gradient in the region (explaining 70% of the first axis of the PCA). We estimated these curves using local least square regressions between probabilities of presences and temperature. We used the 'loess' function (Cleveland *et al.* 1992).

RESULTS

Nested vs non-nested models of species' abundances across sites

The nested framework improved our ability to predict abundance irrespective of the set of variables used and the focal species (see Supporting Information Fig. II.S5). The performance of the nested model was better than the direct model (without the nested framework) in 99% of the cases among all models, repetitions and focal species, with an average increase for the Hanssen-Kuipers discriminant equal to 0.26.

Is it useful to integrate biotic interactions and dispersal into SDMS?

The comparison of the performance of the three models (AC, AD and ACD) with the model that only uses regional environmental filters (A) demonstrated the importance of biotic interactions and dispersal to explain the species' abundances across sites (Fig. II.3). In general, the inclusion of co-occurrence indices (i.e. biotic interactions) was sufficient to significantly improve the model performance. For some species, neither dispersal nor biotic interactions were relevant, whereas their interaction greatly improved the performance of models (e.g. *Ranunculus glacialis, Phragmites australis*, Fig. II.3). Finally, only one species showed no improvement using the proposed indices (*Festuca paniculata,* Fig.II.3).

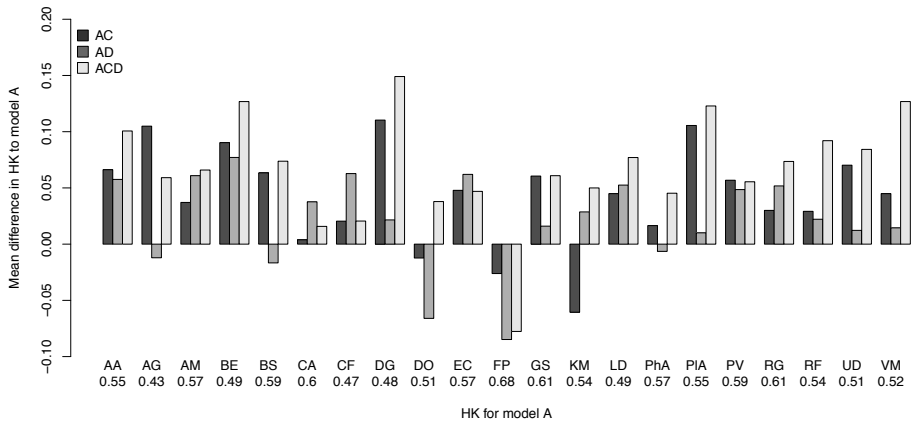

Fig. II.3 Comparison between model A and models AC, AD and ACD. Each bar represents the average difference across all repetitions between the predictive accuracy of model A and the models AC, AD and ACD. Accuracy was measured using the Hanssen-Kuipers discriminant (HK), which varies from 0 to 1 for perfect fit. The numeric values on the X-axis are the mean predictive accuracy of model A. The following abbreviations are used to name the species: AA=*Abies alba,* AG= *Alnus glutinosa,* AM=*Arnica montana,* BE=*Bromus erectus,* BS=*Buxus sempervirens,* CA=*Cacalia alliariae,* CF=*Carex ferruginae,* DG=*Dactylis glomerata,* DO=*Dryas octopetala,* EC=*Euphorbia cyparissias,* FP=*Festuca paniculata,* GS=*Geranium sempervirens,* KM=*Kobresia myosuroides,* LD=*Larix decidua,* PhA=*Phragmites australis,* PlA=*Plantago alpina,* PV=*Polygonum viviparum,* RG=*Ranunculus glacialis,* RF=*Rhododendron ferrugineum,* UD=*Urtica dioica,* VM=*Vaccinium myrtillus*.

Disentangling species abundance and species presence-absence drivers

The separate analysis of variable importance at each model step highlighted major differences in the main drivers of presence-absence or abundance (Fig. II.4). In general, dispersal was relatively important in predicting presence or absence but less for the abundance class where presence was expected (Fig.II.4). The most important biotic interaction index was the repulsion one, followed by the community aggregated C-score, and the attraction index for some species. The niche overlap index was a poor predictor of both presence-absence and abundance. The biotic interactions indices were more important (for all species) in the second step of the model in predicting the abundance class where presence was expected. For instance, *Bromus erectus* well illustrated these results (Fig. II.4). Dispersal was more important for presence-absence, and the importance of biotic interactions increased for abundance. Abiotic variables, although they varied in relative importance between species, were relevant to both modelling steps.

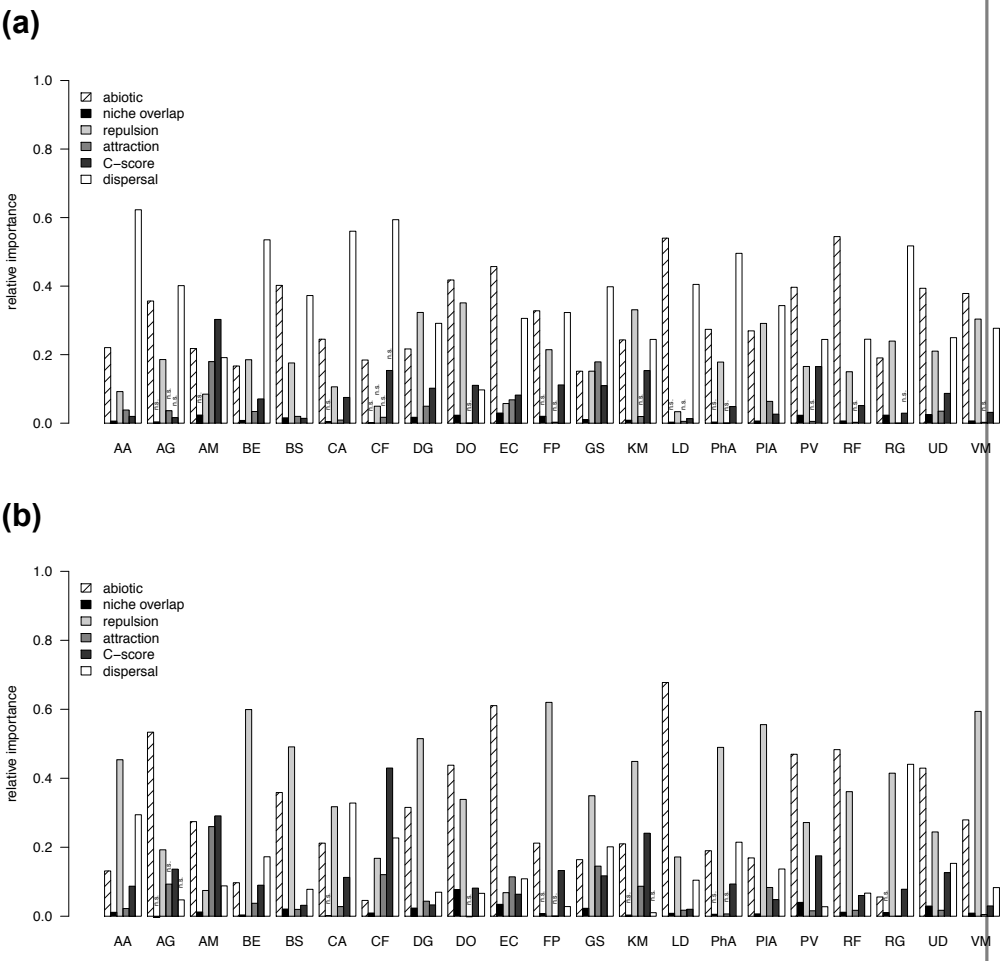

Fig. II.4 Importance of variables. Each barplot represents the relative importance of each variable or group of variables. The relative importance of each abiotic variable was added together. Species abbreviations are the same as for Fig. II.3. Non-significant variables are marked with n.s. **(a)** Importance of variables to explain presence-absence distribution (modelling step 1). **(b)** Importance of variables to explain abundance distribution (modelling step 2).

Biotic interactions and dispersal effects on species' abiotic niches

Our modelling framework allowed us to visualise the effects of the different indices on the abiotic niche space (e.g. *Bromus erectus* in Fig. II.5, other species in Supporting Information Fig. II.S7). For *Bromus erectus*, we found that the realized abiotic niche lies in drier and warmer places than the average of the sampled plots (Fig. II.5a). Using a comparison between the realized niche and a prediction with no dispersal, we identified abiotic conditions of sources and sinks (Fig. II.5b). Surprisingly, sources were located where the density of presences was relatively low (Figs. II.5a and II.5b). Interestingly, sources corresponded to high abundance and sinks to lower abundance (Figs. II.5a and II.5b). With a release of biotic interactions, the abiotic niche did not expand significantly but became denser, particularly in the warmer part of the gradient (Figs II.5c), suggesting there is competition in these areas (red, Fig. II.5c, right panel). At the colder edge of the niche, the density decreased, pointing to positive effects of biotic interactions (green, Fig II.5c, right panel). Some sinks were potentially due to biotic interactions, as they occurred in the same abiotic region as negative biotic interactions (Figs II.5b and II.5c).

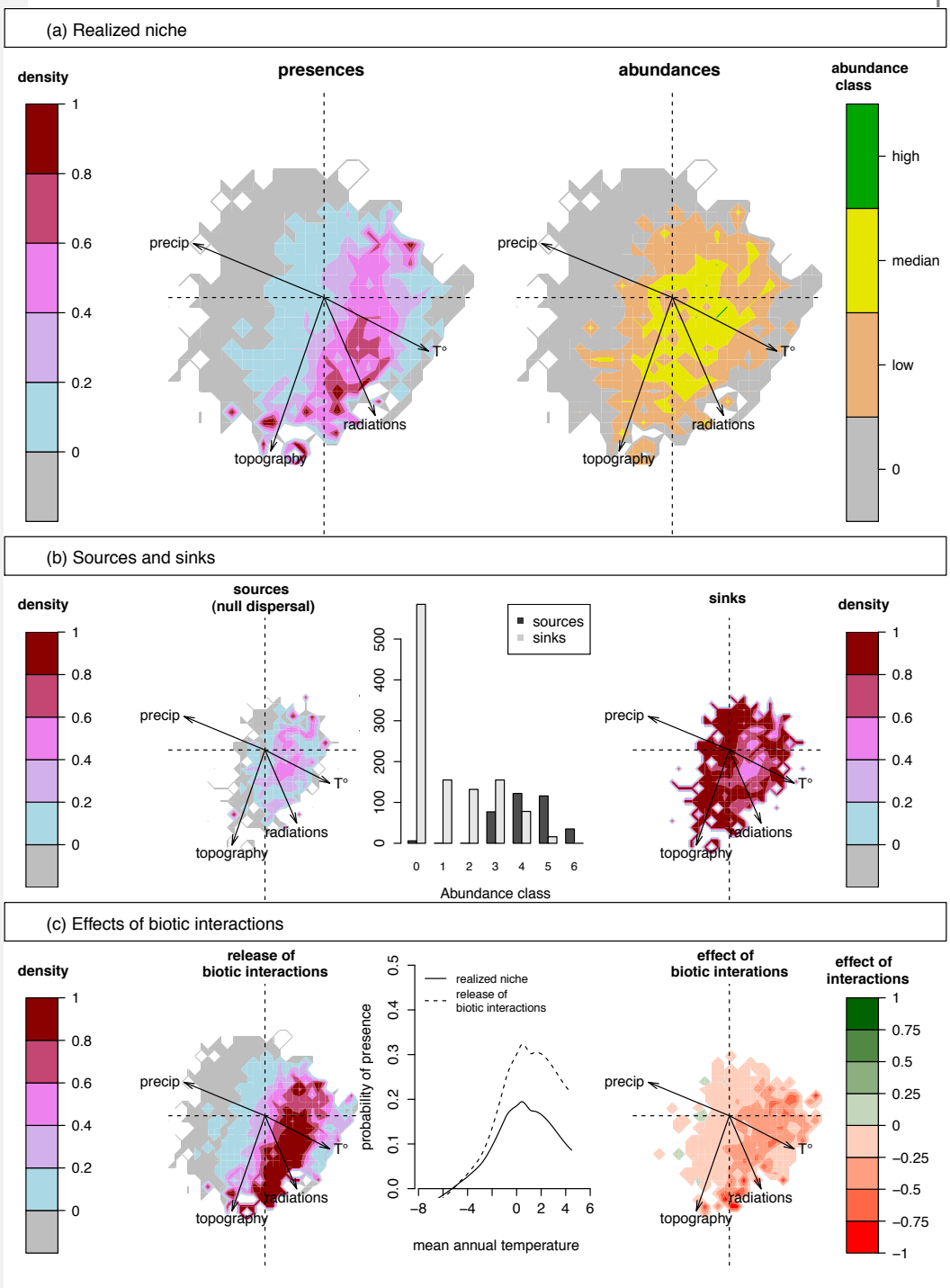

Fig. II.5 Effects of the different drivers on the abiotic niche for *Bromus erectus*. The abiotic niche space is represented by the first two axes (53% of inertia) of a PCA of the abiotic variables. **(a)** Realized niche. Predictions of model ACD. Left: density of predicted presences normalized by the number of sample plots within each grid cell. Right: third quartile of predicted abundance class within each grid cell. Low: <5% cover; Medium: 5% to 25% cover; High:>25% cover. **(b)** Left/right: Proportion of sources/sinks among predicted presences. Middle: abundances in source and sink plots. **(c)** Effect of biotic interactions. Left: density of predicted presences with co-occurrence indices equalling zero. Right: negative and positive effects of the biotic interactions.

DISCUSSION

We proposed and tested a comprehensive framework for investigating mechanisms underlying species distributions and their abundances. Firstly, we demonstrated that the nested modelling structure greatly improves our understanding of distribution and abundance, increasing model performance for all species studied here. Secondly, our nested framework allowed us to show that the ranking in variable importance was reversed between presence-absence and abundance when presence was expected, supporting the hypothesis that different processes were intertwined. Thirdly, we showed that including the three groups of drivers (abiotic, biotic and dispersal) in the same model could offer insights into the mechanisms of community assembly and revealed how they ultimately shape the realized niche from the abiotic niche of species.

Biotic interactions

We showed that community-scale effects of biotic interactions were more important for the second modelling step in explaining abundance when presence was established. This result supports the hypothesis that mechanisms underlying abundance variations occur at community scale, which is where species interact. In our example (*Bromus erectus*), the interaction with the community is essentially negative, particularly at the warm edge of the abiotic niche (Fig. II.5d) where the environment is suitable for a large number of species. Moreover, co-occurrence indices associated to repulsion are relatively important for the abundance model step (Fig. II.4b). These results suggest that co-occurrence indices are strongly related to negative biotic interactions, such as competition for resources (Chase & Leibold 2003; Soberon 2007). At the same time, we observed positive effects of biotic interactions at the colder edge of the abiotic niche. This may be the consequence of facilitation, which has been suggested to be an important factor of species coexistence in harsh conditions (Choler *et al.* 2001; Callaway *et al.* 2002).

Observed species co-occurrence has long been used to infer community assembly rules (Gilpin & Diamond 1982; Gotelli & McCabe 2002) and several co-occurrence based indices have been used in SDMs as a proxy

for unmeasured abiotic conditions and species interactions (Leathwick 2002; Cottenie 2005; Araujo & Luoto 2007; Meier *et al.* 2010). The main limitation of these approaches is that non co-occurring species pairs could be interpreted either as the result of competitive exclusion or different species' environmental niches (Gilpin & Diamond 1982). Here, we propose to use a comparison between observed and expected community composition to tease apart the effects of environment from those of competition (Chesson 2000a; Chase & Leibold 2003; Silvertown 2004). Moreover, these new metrics allow distinguishing between positive (attraction) and negative (repulsion) effects. In further studies, it would also be interesting to separate the cases where a species undergoes competition (or facilitation) from the situation where the species has the strongest competitive ability (or facilitate other species) (Tab. II.1). These indices still cannot distinguish biotic interactions from micro-environmental conditions effects that may have a prominent role (e.g. topographical heterogeneity inducing thermal differences, Scherrer & Körner 2011). For instance, the co-occurrence indices for *Phragmites australis* possibly relate to specific local abiotic conditions (small wetlands) whereas the repulsion index for *Dactylis glomerata,* a common and widely distributed grass, probably reveals its competitive strategy. Because we will never be able to measure every abiotic variable at community scale, the attraction and repulsion indices provide an interesting proxy for describing local abiotic and biotic environments. Their influence on species distributions are stronger than the niche overlap index and are relatively easy to interpret in respect to the aggregated C-score.

The construction of the expected species pool is crucial for most of the proposed indices and requires particular attention. As we assume no dispersal limitation when calculating the expected species pool, we may overestimate expected species richness at inaccessible sites. For some species, important limiting variables might also be missing or imprecise (e.g. soil data). These species would thus be wrongly added to the species pool. However, this bias cannot explain alone the poor predictive power of the niche overlap index because the expected species pool is also used

to build the repulsion index. This pattern might suggest that competition does occur in few plots only, while in the others plots, spatial and temporal environmental heterogeneity allow species coexistence (Silvertown, 2004). Finally, although competition would preferentially occur between functionally similar species, we did not consider species identity. The addition of weights based on functional traits to our indices might be worth considering, as they may be directly linked to resource acquisition or exploitation (Lavorel & Garnier 2002).

Dispersal

There are now several studies supporting the importance of dispersal on species distributions (e.g. Bahn & McGill 2007). This is, however, usually approximated by spatial autocorrelation functions (e.g. Borcard *et al.* 1992), generally built with little or no attention to the true spatial processes that drive biogeographical patterns. Although the fraction of variance explained by these variables is often interpreted as the spatial signature of dispersal limitations (Beale *et al.* 2008), this spatial structure could also result from unaccounted spatially auto-correlated environmental factors (Gravel *et al.* 2008; Araujo *et al.* 2009). Here, we had an underlying hypothesis with an explicit formulation based on species-specific dispersal distances, which allows us to progress in our understanding of the processes driving spatial distribution. Confusion may however still arise when missing spatially autocorrelated abiotic drivers operate at the same spatial scale as dispersal mechanisms (Cottenie 2005).

Our study showed that dispersal mechanisms were more important for determining presence-absence patterns, suggesting strong dispersal limitations. Far from its geographical range, a species is systematically predicted to be absent because it cannot reach the site, even if the environment is suitable. It can introduce a bias in the relationship between species distribution and abiotic variables, because in these sites, abiotic constraints might be neglected. It is not possible however to reveal the real cause of such absences if all sampled plots with similar abiotic conditions are systematically far from the species geographical

distribution. Ideally, to estimate the true relationship between species distribution and abiotic variables (i.e. the fundamental abiotic niche), the sampling should be homogeneous not only in relation to the abiotic variables but also spatially.

The importance of the dispersal index in the second model step highlights the implication of dispersal mechanisms at local scale, such as source-sink dynamics. Interestingly, the sources identified in our case study (and three other examples, Fig. II.S7) are not related to the density of presence but to species' abundance (Fig. II.5). These results support the source-sink theory, which predicts species occurrences in unsuitable habitat if immigration from surrounding source populations is sufficiently large (Pulliam 2000).

Species distribution and abiotic niches

Species distribution models generally use topoclimatic predictors only (Guisan & Zimmermann 2000). Consequently, the relationship they model between abiotic variables and the distribution includes at the same time abiotic constraints, dispersal mechanisms and interaction between species (Guisan & Zimmermann 2000; Soberon 2007). Here, because we introduced other explicative variables to describe dispersal and species interactions mechanisms, the modelled relationship between abiotic variables and the species distribution is refined and should be closer to the fundamental niche. Although the approximation of the fundamental niche is obviously constrained by the area considered and should be valid only for the gradient sampled, our method refines the relationship between topoclimatic variables and species distribution for our region. Whilst we agree that only experiments can define the fundamental niche (e.g. Vetaas 2002; Kearney & Porter 2009) whereas we only approximate it here, our model allows us to explore the effects of dispersal and biotic interactions on the abiotic niche, including the identification of sources and sinks (Fig. II.5b) and is able to point out potential sites where facilitation or competition have a strong impact (Fig. II.5c).

Perspectives

Our framework extends the boundaries of SDMs and should allow important ecological questions to be addressed. It offers an innovative way to improve our understanding of community assembly processes for large spatial scales and for many species at once, based on largely available data: coarse scale environmental variables, community surveys at the scale of species interactions, and species-specific dispersal abilities. For instance, understanding and predicting species invasion might benefit from this framework, as the potential distribution of the invader species in a region is often unknown because the realized distribution of the species usually reflects the place of introduction, dispersal capability of the species and biotic resistance of the native communities (Gallien *et al.* 2010). More fundamentally, not all species are influenced by the same factors. Applying our framework to a large set of species could help providing general rules or patterns for groups of species. For instance, dominant and generalist species are in theory less likely to be influenced by negative biotic interactions than subordinated species (Boulangeat *et al.* 2012). These relatively old but generally unresolved questions in ecology and biogeography might be now tackled or addressed from a different angle.

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SUPPORTING INFORMATION

1) Details on the datasets

Table II.S1: Species observation data. The following table gives the species number of observation in each abundance class, for each modelled species, over the 8160 sampling plots.

Abundance classes:	0	1	2	3	4	5	6
Abies alba	7427	236	156	144	94	74	29
Alnus glutinosa	8078	26	11	18	13	9	5
Arnica montana	7935	137	55	31	2	0	0
Bromus erectus	7191	224	196	193	186	126	44
Buxus sempervirens	7571	129	105	154	122	63	16
Cacalia alliariae	7813	127	87	73	40	18	2
Carex ferruginea	8052	20	25	21	31	9	2
Dactylis glomerata	7043	568	298	179	61	10	1
Dryas octopetala	7939	67	49	58	31	14	2
Euphorbia cyparissias	7355	587	182	34	2	0	0
Festuca paniculata	7888	93	47	51	51	28	2
Geranium sylvaticum	7386	364	236	136	35	3	0
Kobresia myosuroides	7959	60	42	42	51	6	0
Larix decidua	7839	110	59	45	61	27	19
Phragmites australis	7949	67	45	46	25	9	19
Plantago alpina	7433	199	280	174	57	15	2
Polygonum viviparum	7308	351	353	135	12	1	0
Ranunculus glacialis	7949	130	63	18	0	0	0
Rhododendron ferrugineum	7738	148	83	78	67	33	13
Urtica dioica	7755	204	109	62	22	4	4
Vaccinium myrtillus	7290	204	221	224	159	47	15

Table II.S2: Dispersal parameters. The following table gives the dispersal parameters used in the dispersal model. They have been attributed according to their dispersal class following Vittoz *et. al* (2007).

Species	Dispersal class	d99 (m)	Idd (m)
Abies alba	4	150	1000
Alnus glutinosa	4	150	1000
Arnica montana	3	15	1000
Bromus erectus	4	150	1000
Buxus sempervirens	3	15	1000
Cacalia alliariae	5	500	5000
Carex ferruginea	6	1500	5000
Dactylis glomerata	7	5000	10000
Dryas octopetala	3	15	1000
Euphorbia cyparissias	7	5000	10000
Festuca paniculata	3	15	1000
Geranium sylvaticum	6	1500	5000
Kobresia myosuroides	6	1500	5000
Larix decidua	6	1500	5000
Phragmites australis	5	500	5000
Plantago alpina	6	1500	5000
Polygonum viviparum	1	1	1000
Ranunculus glacialis	4	150	1000
Rhododendron ferrugineum	1	1	1000
Urtica dioica	7	5000	10000
Vaccinium myrtillus	7	5000	10000

Name	Description	Source
Temperature	Annual mean daily monthly mean temperature(°C)	Meteo France[1] 100x100m resolution
Precipitations	Winter precipitations (January to March)(mm)	
Moisture	Moisture index for the growing season (June to August) measured as the balance between gains from precipitation and losses from potential evapo-transpiration ($mm.d^{-1}$)	
Radiation	Potential yearly global radiation, expressing the potential amount of direct and diffuse solar irradiation ($kJ.m^{-2}.d^{-1}$)	
Soil carbon	Percentage of carbon in the bedrock	Soil European Database http://eusoils.jrc.ec.europa.eu/data.html 1kmx1km resolution
Available water capacity	Available water that can be stored in soil and be available for use by plants	
Slope	Slope angle (°)	French Digital elevation model at resolution 50x50m (IGN-France)
Topography	Difference between the average elevation in a circular moving window and the centre cell of the window	
Wetness index	Topographic wetness index (TWI) [2]	
Corine land cover	Corine Land Cover simplified to 7 classes: artificial surfaces (1**), agricultural areas (2**), forest (31*), scrub (32*), open spaces (33*), wetlands (4**) and water bodies (5**)	European Topic Centre on Land Use and Spatial Information. 100mx100m resolution Date of delivery: 14 Sep 2009

Table II.S3: Abiotic variables' description. We provide a detailed description of each abiotic variable and precise the source.

[1] Bénichou, P. and O. Le Breton. 1987. Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. La Météorologie 7:23-34.

[2] TWI=upslope contributing area / tan(slope angle). TWI is an hydrological index developed by Beven and Kirkby 1979. This method calculates the amount of water that runs through a pixel and corrects this for slope in order to have a measure of potential soil humidity. Beven, K. J. and Kirkby, M. J.: A physically based, variable contributing area model of basin hydrology, Hydrol. Sci. Bull., 24, 43–69, 1979.

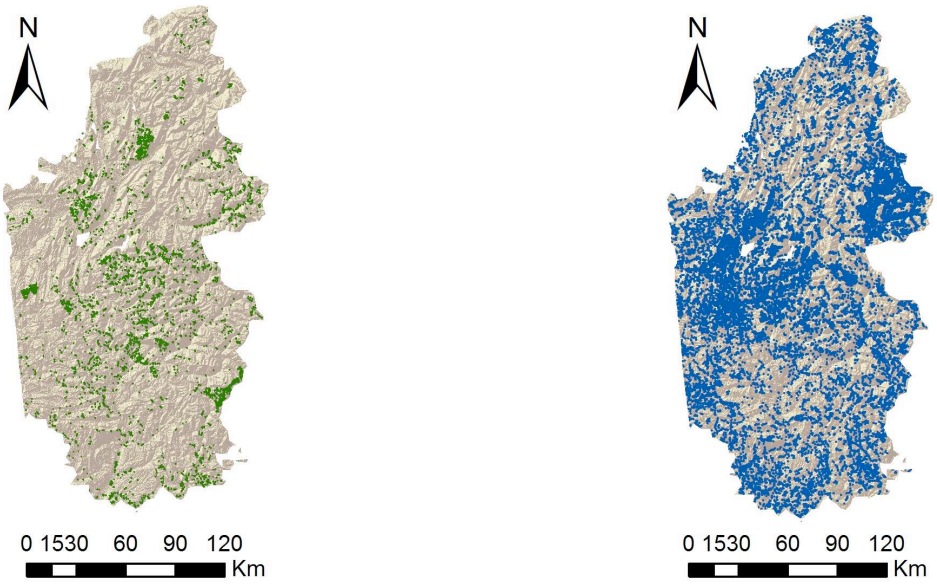


Fig.II.S1 Vegetation datasets. Left: study area with the 8160 community plots where species are modelled. Right : study area with all additional presence-only data, used to build the different indices.

Fig.II.S2 Topo-climatic variables distributions. The following maps show variable spatial distributions. The geographic scale is in meters. The average temperature is in °C, the winter precipitation is in mm, the moisture index of the growing season is in $mm.d^{-1}$, the potential yearly global radiation is in $kJ.m^{-2}.d^{-1}$, the available water capacity is in mm and the carbon in the bedrock is in percentage, the topography is in meters, the topographic wetness index has no units, and the slope angle is in degree.

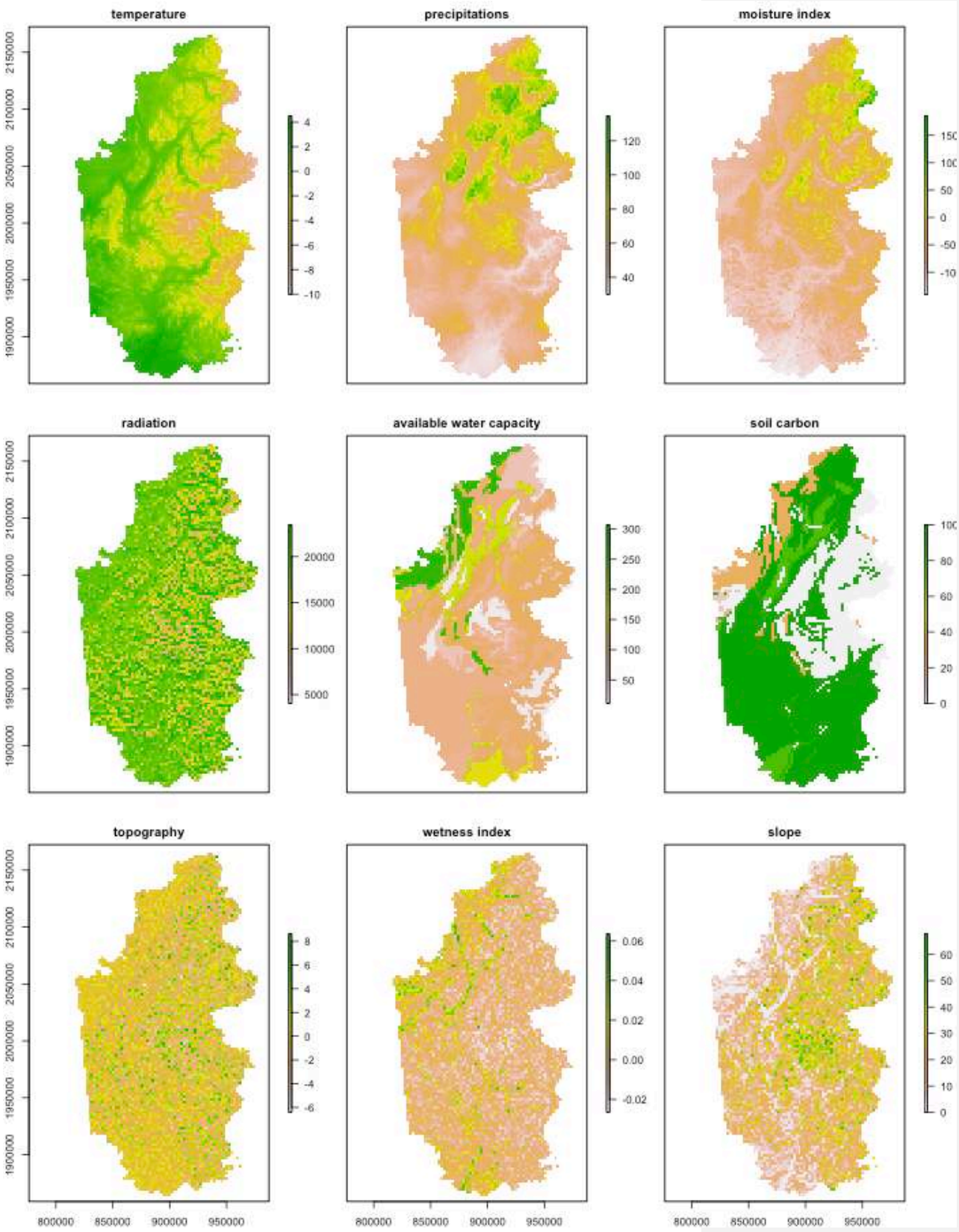
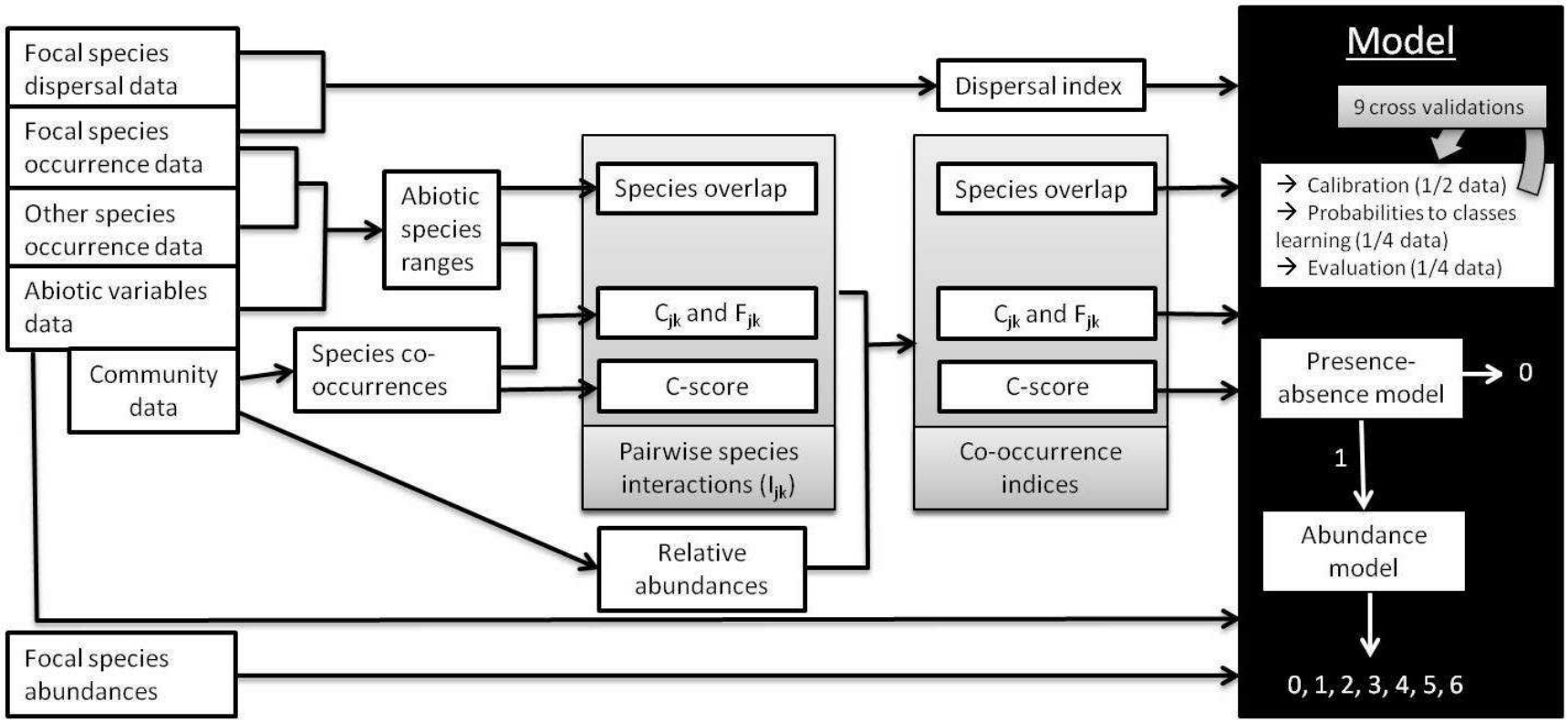


Fig. II.S3. Model workflow. From vegetation databases abiotic variables and community composition, we derived the different co-occurrence indices. The resulting indices were then used as predictor variables in the main model. This model consists in two steps. The first step is a classical presence-absence distribution model and the second step models abundance classes for the sites where presence has been predicted by the first step. We used a cross-validation approach, dividing the dataset into three parts in each repetition, for calibration (50%), transformation into classes (25%) and evaluation (25%). For presence-absence, the binary transformation into presence-absence was based on the threshold optimizing the True Skill Statistic. For abundance classes, it was based on weights optimizing the Hanssen-Kuipers score (eq. II.S1).



Eq. II.S1 Calculation of the Hanssen-Kuipers discriminant score.

$$HK = \frac{\frac{1}{N}\sum_i n(P_i, O_i) - \frac{1}{N^2}\sum_i N(P_i).N(O_i)}{1 - \frac{1}{N^2}\sum_i (N(O_i))^2}$$

where N is the total number of sites, $n(P_i, O_i)$ is the number of predictions that match with obervations for the class i, $N(O_i)$ is the number of observations in the class i and $N(P_i)$ is the number of predictions in the class i.

Eq. II.S2 Calculation of variable importance.

The variable importance for the variable x is calculated using the Out-Of-Bag (OOB) sample which is a subsample of the data that has been put aside during the calibration and is used as independant data to evaluate the model. The variable importance is the mean difference in accuracy between normal predictions and predictions with a randomly permuted variable x. For each permuation, the variable importance VI is equal to :

$$VI_x = \frac{1}{N}\sum_i n(P_i, O_i) - \frac{1}{N}\sum_i n(P_i^x, O_i)$$

where N is the number of plots in the OOB sample, $n(P_i, O_i)$ is the number of predictions that match with observations for the class i and P^x is the prediction vector obtained after randomly permuting the predictor variable x.

3) Intermediate results

Table II.S4: Correlations between proposed indices and topo-climatic variables. The following table gives the Pearson correlations in sampled sites between the proposed indices and all topo-climatic variables, for the 21 focal species. Highest correlations (above 0,6) are highlighted. T°: average temperature, Precip: winter precipitations, Moist:moisture index for the growing season, Rad: potential yearly radiation, WC: soil available water capacity, Carbon: percentage of carbon in the bedrock, topo: topography, wetness: topographic wetness index, slope.

	T°	Precip.	Moist.	Rad.	WC	Carbon	topo	wetness	slope
Abies alba									
species pool	0.14	-0.01	-0.15	0.00	-0.09	0.10	-0.08	-0.02	-0.04
repulsion	-0.11	0.08	0.07	0.05	-0.09	-0.01	0.01	-0.06	0.03
attraction	0.09	0.09	0.05	-0.07	0.08	0.04	-0.01	-0.01	0.05
Cscore	-0.23	-0.01	0.07	0.06	-0.11	-0.03	0.09	-0.07	-0.02
dispersal	0.12	0.22	0.14	-0.17	-0.02	0.15	0.04	-0.14	0.14
Alnus glutinosa									
species pool	0.48	-0.30	-0.52	0.15	0.06	0.20	-0.12	0.14	-0.19
repulsion	**0.67**	-0.26	-0.51	0.20	0.25	0.26	-0.06	0.11	-0.08
attraction	0.33	-0.22	-0.28	0.07	0.13	0.09	-0.04	0.33	-0.20
Cscore	-0.17	0.10	0.14	-0.04	-0.10	0.01	0.11	-0.17	0.09
dispersal	0.27	-0.11	-0.17	0.05	0.28	-0.06	-0.06	0.26	-0.20
Arnica montana									
species pool	-0.28	0.17	0.18	-0.12	-0.30	-0.01	-0.05	-0.19	0.13
repulsion	-0.57	0.42	0.56	-0.24	-0.29	-0.10	0.13	-0.35	0.27
attraction	-0.22	0.02	0.10	0.00	-0.13	0.00	0.03	-0.03	-0.04
Cscore	0.01	0.01	0.00	-0.02	-0.02	0.06	0.07	-0.10	0.07
dispersal	-0.30	0.23	0.32	-0.04	-0.05	-0.24	0.02	-0.11	0.10
Bromus erectus									
species pool	0.16	-0.04	-0.18	0.01	-0.08	0.11	-0.09	-0.01	-0.05
repulsion	0.56	-0.15	-0.35	0.07	0.22	0.24	-0.03	0.11	-0.04
attraction	0.03	0.09	0.04	0.00	0.03	-0.02	-0.05	0.03	-0.04
Cscore	-0.23	0.17	0.23	-0.13	-0.11	-0.02	0.11	-0.15	0.10
dispersal	0.36	-0.29	-0.43	0.26	0.04	0.17	-0.03	0.05	-0.11
Buxus sempervirens									
species pool	0.45	-0.28	-0.49	0.14	0.04	0.19	-0.12	0.13	-0.17
repulsion	**0.72**	-0.24	-0.53	0.20	0.27	0.22	-0.13	0.25	-0.17
attraction	0.39	-0.21	-0.29	0.09	0.18	0.10	-0.04	0.28	-0.15
Cscore	-0.29	0.16	0.24	-0.09	-0.14	-0.05	0.09	-0.11	0.04
dispersal	0.57	-0.30	-0.47	0.15	0.17	0.33	0.05	-0.01	-0.08
Cacalia alliariae									
species pool	-0.09	0.07	0.02	-0.06	-0.22	0.04	-0.07	-0.12	0.06
repulsion	-0.41	0.35	0.43	-0.16	-0.22	-0.05	0.12	-0.29	0.22
attraction	-0.30	0.27	0.33	-0.09	-0.13	-0.04	0.09	-0.16	0.15
Cscore	-0.14	-0.01	0.03	0.04	-0.08	0.02	0.10	-0.09	0.01
dispersal	-0.03	0.41	0.37	-0.30	-0.02	0.02	0.08	-0.17	0.18
Carex ferruginea									
species pool	0.06	0.05	-0.07	-0.03	-0.12	0.08	-0.07	-0.06	0.00
repulsion	-0.48	0.41	0.52	-0.25	-0.24	-0.08	0.13	-0.31	0.25
attraction	-0.04	0.10	0.09	-0.01	-0.02	0.00	0.02	-0.03	0.00
Cscore	-0.07	0.04	0.05	-0.03	-0.05	0.03	0.09	-0.11	0.05
dispersal	-0.12	0.52	0.45	-0.12	-0.02	0.05	0.13	-0.18	0.15
Dactylis glomerata									
species pool	0.14	-0.02	-0.16	0.00	-0.09	0.10	-0.09	-0.02	-0.04
repulsion	0.31	-0.02	-0.14	-0.01	0.10	0.22	0.07	-0.09	0.11
attraction	0.11	-0.10	-0.16	0.18	-0.01	0.06	0.03	-0.06	0.05
Cscore	-0.17	0.10	0.16	-0.08	-0.09	0.01	0.13	-0.17	0.12
dispersal	0.39	0.00	-0.20	0.15	0.19	0.00	0.00	0.09	-0.08
Dryas octopetala									
species pool	0.09	0.02	-0.11	-0.02	-0.11	0.09	-0.08	-0.04	-0.02
repulsion	-0.52	0.39	0.51	-0.21	-0.27	-0.10	0.12	-0.32	0.23
attraction	0.03	-0.03	-0.04	0.02	0.01	-0.01	-0.01	0.01	-0.03
Cscore	0.00	0.05	0.03	-0.03	-0.02	0.05	0.06	-0.08	0.03
dispersal	-0.42	0.11	0.31	-0.19	-0.10	-0.22	0.00	-0.18	0.20
Euphorbia cyparissias									
species pool	0.21	-0.11	-0.26	0.04	-0.09	0.13	-0.10	0.01	-0.06
repulsion	-0.13	0.15	0.18	-0.12	-0.10	0.08	0.12	-0.25	0.15
attraction	0.01	0.07	0.04	0.02	0.02	-0.03	-0.05	0.04	-0.06
Cscore	-0.12	0.10	0.13	-0.08	-0.06	0.02	0.09	-0.11	0.05
dispersal	0.13	-0.29	-0.29	0.11	-0.03	0.03	-0.03	-0.04	0.10

	T°	Precip.	Moist.	Rad.	WC	Carbon	topo	wetness	slope
Festuca paniculata									
species pool	-0.27	0.16	0.17	-0.12	-0.30	-0.01	-0.06	-0.18	0.12
repulsion	-0.51	0.38	0.51	-0.24	-0.28	-0.06	0.12	-0.32	0.24
attraction	-0.03	-0.02	0.00	0.00	-0.01	-0.02	-0.04	-0.01	0.03
Cscore	-0.03	0.04	0.04	-0.04	-0.03	0.06	0.08	-0.11	0.06
dispersal	-0.35	-0.06	0.10	-0.01	-0.14	-0.31	-0.07	-0.09	0.15
Geranium sylvaticum									
species pool	0.09	-0.04	-0.15	0.00	-0.14	0.10	-0.09	-0.04	-0.02
repulsion	-0.51	0.32	0.45	-0.17	-0.27	-0.06	0.14	-0.35	0.25
attraction	-0.02	0.18	0.15	-0.09	0.03	-0.03	0.00	-0.04	0.02
Cscore	-0.06	0.01	0.03	0.00	-0.05	0.05	0.11	-0.12	0.06
dispersal	-0.20	0.36	0.37	-0.19	-0.06	-0.21	0.00	-0.17	0.22
Kobresia myosuroides									
species pool	0.09	0.01	-0.12	-0.02	-0.11	0.09	-0.08	-0.04	-0.02
repulsion	**-0.70**	0.37	0.57	-0.19	-0.33	-0.19	0.12	-0.30	0.21
attraction	-0.11	-0.03	0.03	-0.01	-0.11	0.04	-0.02	0.00	0.00
Cscore	0.04	0.05	0.01	-0.02	0.00	0.05	0.06	-0.08	0.05
dispersal	-0.57	0.06	0.33	-0.12	-0.14	-0.28	0.04	-0.13	0.08
Larix decidua									
species pool	0.13	-0.01	-0.14	-0.01	-0.09	0.10	-0.08	-0.03	-0.03
repulsion	-0.34	0.27	0.33	-0.12	-0.20	-0.01	0.12	-0.30	0.19
attraction	-0.15	0.08	0.07	0.09	-0.09	-0.08	0.08	-0.16	0.15
Cscore	-0.08	0.05	0.06	-0.02	-0.06	0.04	0.09	-0.10	0.03
dispersal	-0.20	-0.22	0.03	-0.19	-0.10	-0.16	-0.12	-0.06	0.18
Phragmites australis									
species pool	0.15	-0.03	-0.18	0.01	-0.08	0.11	-0.09	-0.01	-0.05
repulsion	0.37	-0.12	-0.26	0.10	0.11	0.20	0.04	-0.03	0.00
attraction	0.03	-0.03	-0.04	0.01	0.01	0.00	-0.02	0.04	-0.03
Cscore	-0.16	0.11	0.14	-0.05	-0.10	0.02	0.11	-0.17	0.11
dispersal	0.36	-0.16	-0.27	0.08	0.31	0.00	-0.10	0.41	-0.33
Plantago alpina									
species pool	0.08	0.02	-0.10	-0.02	-0.11	0.08	-0.08	-0.05	-0.01
repulsion	**-0.67**	0.43	**0.61**	-0.25	-0.31	-0.22	0.10	-0.37	0.30
attraction	-0.22	0.16	0.19	0.03	-0.09	-0.01	0.10	-0.12	0.06
Cscore	0.13	0.01	-0.04	-0.02	0.05	0.07	0.06	-0.08	0.08
dispersal	-0.57	0.08	0.31	-0.08	-0.35	-0.10	0.01	-0.11	0.06
Polygonum viviparum									
species pool	0.11	0.00	-0.13	-0.01	-0.10	0.09	-0.08	-0.04	-0.03
repulsion	**-0.70**	0.40	0.59	-0.22	-0.32	-0.21	0.14	-0.40	0.29
attraction	-0.05	0.19	0.19	-0.14	0.01	-0.03	0.01	-0.07	0.06
Cscore	0.12	0.02	-0.04	-0.01	0.04	0.08	0.06	-0.08	0.07
dispersal	**-0.67**	0.10	0.43	-0.24	-0.29	-0.23	-0.09	-0.08	0.08
Ranunculus glacialis									
species pool	0.10	-0.01	-0.13	-0.01	-0.11	0.09	-0.08	-0.04	-0.03
repulsion	**-0.71**	0.32	0.54	-0.16	-0.33	-0.19	0.12	-0.27	0.17
attraction	-0.02	0.01	0.01	-0.02	0.00	-0.02	0.02	-0.02	0.01
Cscore	-0.01	0.07	0.04	-0.02	-0.03	0.05	0.07	-0.10	0.06
dispersal	-0.35	0.07	0.21	-0.06	-0.11	-0.12	0.11	-0.12	0.06
Rhododendron ferrugineum									
species pool	-0.21	0.14	0.13	-0.11	-0.27	0.01	-0.06	-0.16	0.11
repulsion	-0.50	0.40	0.51	-0.21	-0.28	-0.05	0.10	-0.31	0.24
attraction	-0.08	0.23	0.22	-0.13	0.01	-0.03	0.03	-0.09	0.07
Cscore	0.00	-0.02	-0.03	0.02	-0.04	0.08	0.07	-0.08	0.02
dispersal	-0.35	0.32	0.44	-0.30	-0.03	-0.45	-0.01	-0.19	0.27
Urtica dioica									
species pool	0.14	-0.02	-0.16	0.00	-0.09	0.10	-0.08	-0.02	-0.04
repulsion	-0.01	0.09	0.05	0.00	-0.05	0.11	0.11	-0.22	0.13
attraction	-0.01	0.05	0.05	-0.06	-0.01	0.01	-0.01	-0.03	0.05
Cscore	-0.14	0.05	0.09	0.00	-0.08	0.02	0.12	-0.13	0.05
dispersal	0.28	0.12	-0.02	-0.05	0.19	-0.03	0.04	0.00	0.00
Vaccinium myrtillus									
species pool	0.13	-0.06	-0.19	0.01	-0.12	0.11	-0.09	-0.02	-0.03
repulsion	-0.51	0.25	0.40	-0.12	-0.29	-0.06	0.09	-0.28	0.18
attraction	0.01	0.01	0.00	0.01	0.02	-0.03	0.04	-0.03	0.01
Cscore	-0.03	-0.07	-0.06	0.06	-0.05	0.07	0.06	-0.06	0.00
dispersal	-0.17	0.47	0.40	-0.16	-0.03	-0.31	0.10	-0.23	0.22

Table II.S5: Sensitivity to the dispersal distance class. The table shows Pearson correlations between various estimates of the dispersal index for *Geranium sempervirens*. Each time, we estimated the dispersal index using distance parameters from a different dispersal class (1, 3, 4, 5, 6, and 7).

Dispersal class	1	3	4	5	6	7
1	1.00	1.00	0.73	0.84	0.95	0.98
3		1.00	0.73	0.84	0.95	0.98
4			1.00	0.97	0.88	0.77
5				1.00	0.96	0.86
6					1.00	0.95
7						1.00

Fig. II.S4. Species distributions for the dispersal model. These distributions are the result of the random forest model used to build the dispersal index, for the 21 focal species. They show the spatial configuration of realized species distributions.

4) Effects of the nested modelling method

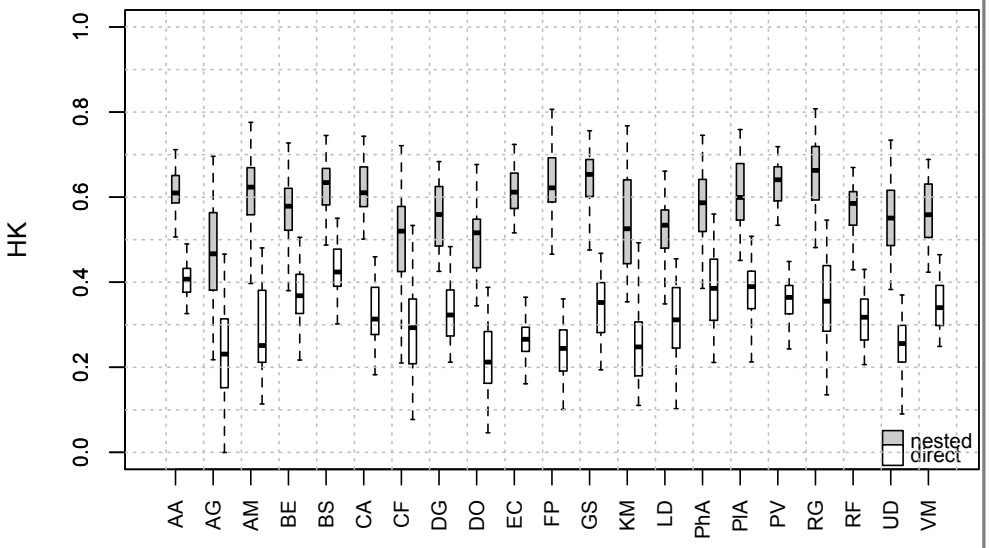


Fig.II.S5 Effect of the nested modelling method on model evaluations. The following figures show the variation in model evaluation across four models and nine repetitions, for each modelled species. The following abbreviations are used to name the species: AA=*Abies alba,* AG= *Alnus glutinosa,* AM=*Arnica montana,* BE=*Bromus erectus,* BS=*Buxus sempervirens,* CA=*Cacalia alliariae,* CF=*Carex ferruginae,* DG=*Dactylis glomerata,* DO=*Dryas octopetala,* EC=*Euphorbia cyparissias,* FP=*Festuca paniculata,* GS=*Geranium sempervirens,* KM=*Kobresia myosuroides,* LD=*Larix decidua,* PhA=*Phragmites australis,* PlA=*Plantago alpina,* PV=*Polygonum viviparum,* RG=*Ranunculus glacialis,* RF=*Rhododendron ferrugineum,* UD=*Urtica dioica,* VM=*Vaccinium myrtillus.* The white boxplots are evaluations of direct modelling, which is a direct fit of abundance classes. The grey boxplots are evaluations of nested modelling, where abundance classes are fitted only in sites where presence is predicted. The evaluation method is the Hanssen-Kuipers discriminant (HK), which varies from 0 to 1 for perfect fit.

5) Variable importance

(a): Variable importance for presence-absence step

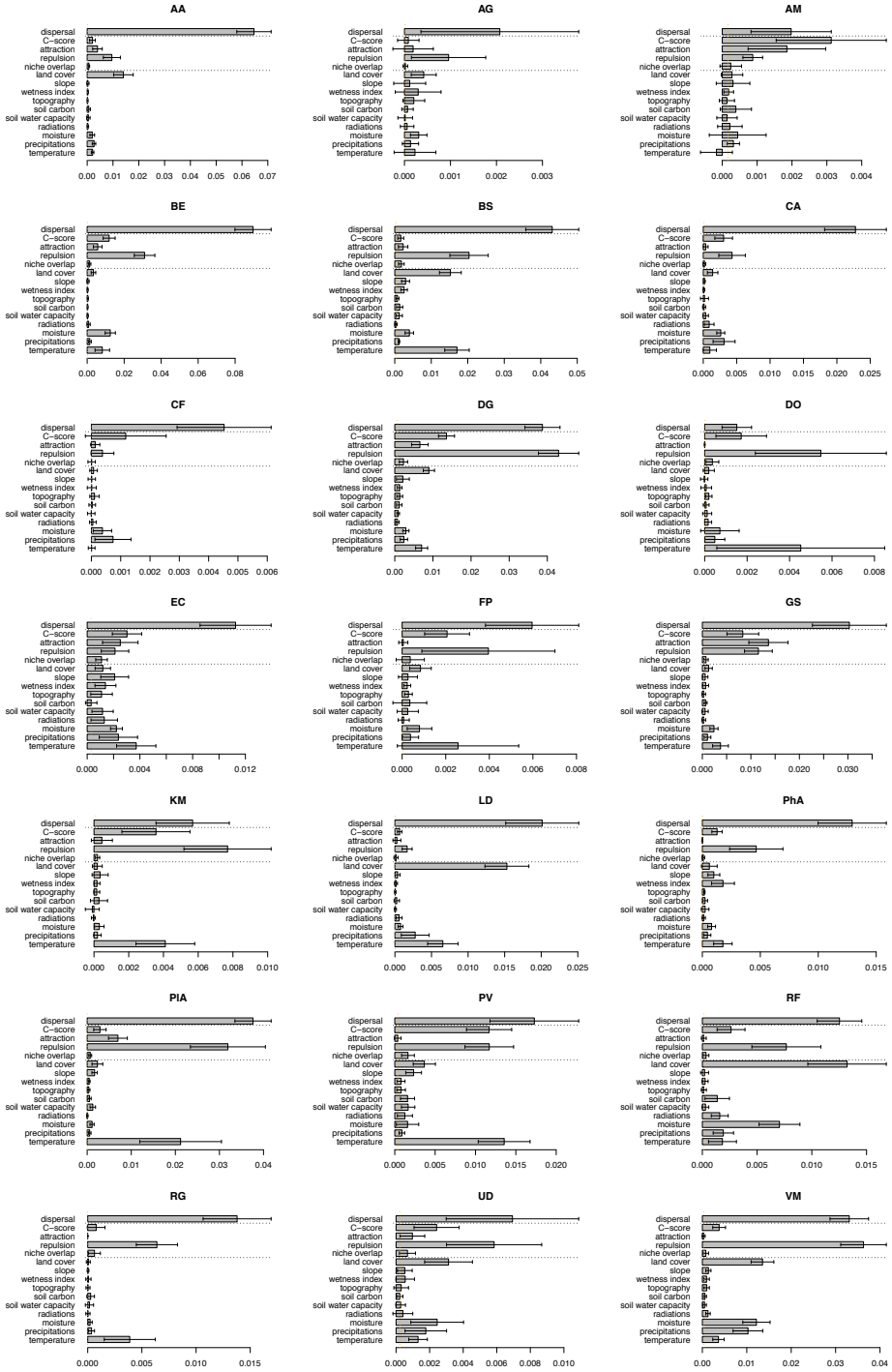
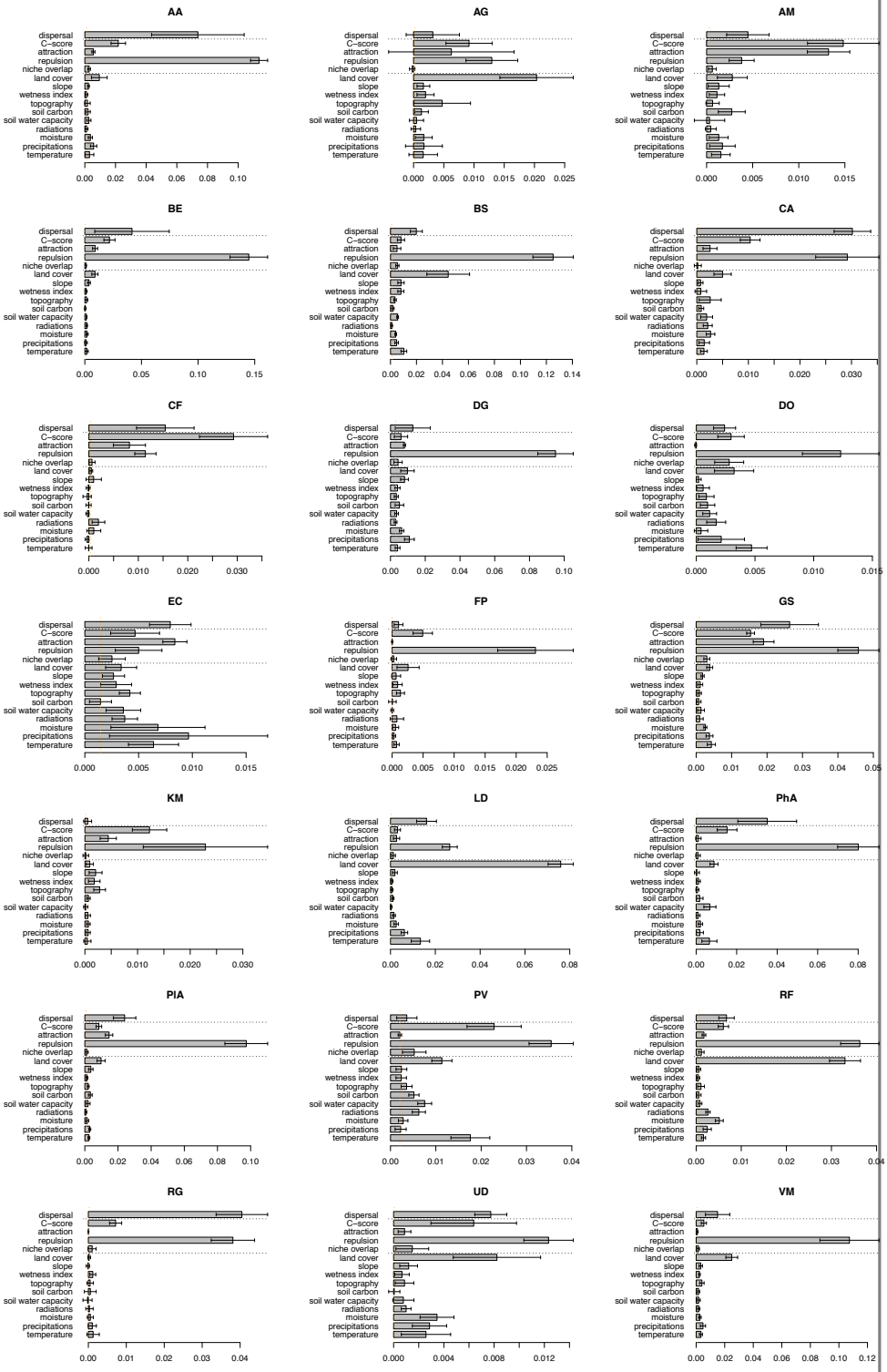


Fig. II.S6: Detailed variable importance. The following figures show the variable importance for each species, measured as the average change in model accuracy across repetitions when the focal variable is randomized. The segments show confidence intervals (mean+/-1.96*sd) across repetitions. A variable was considered not significant when its importance confidence interval included zero.

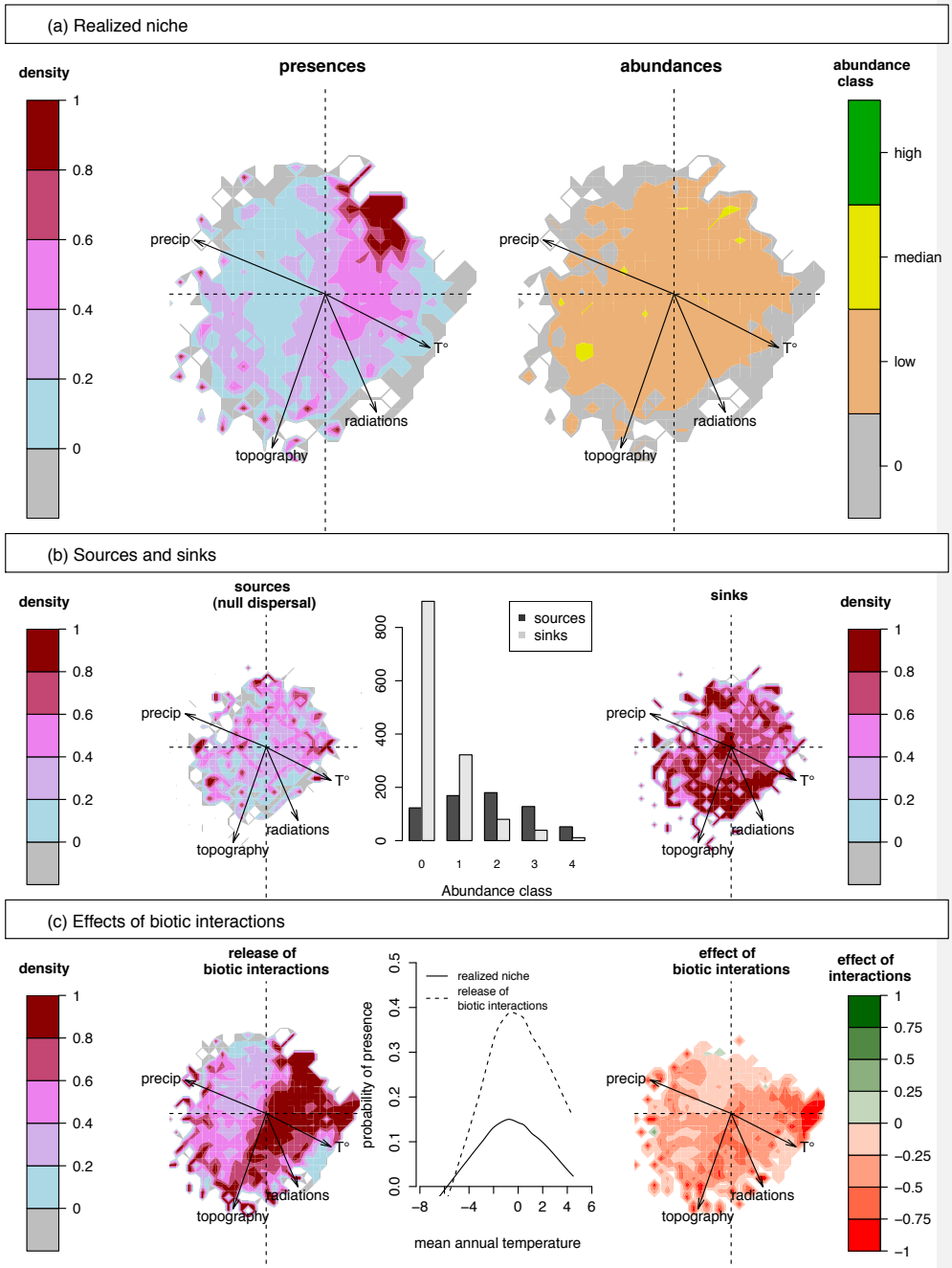
(b) Variable importance for abundance variation (2nd modelling step).



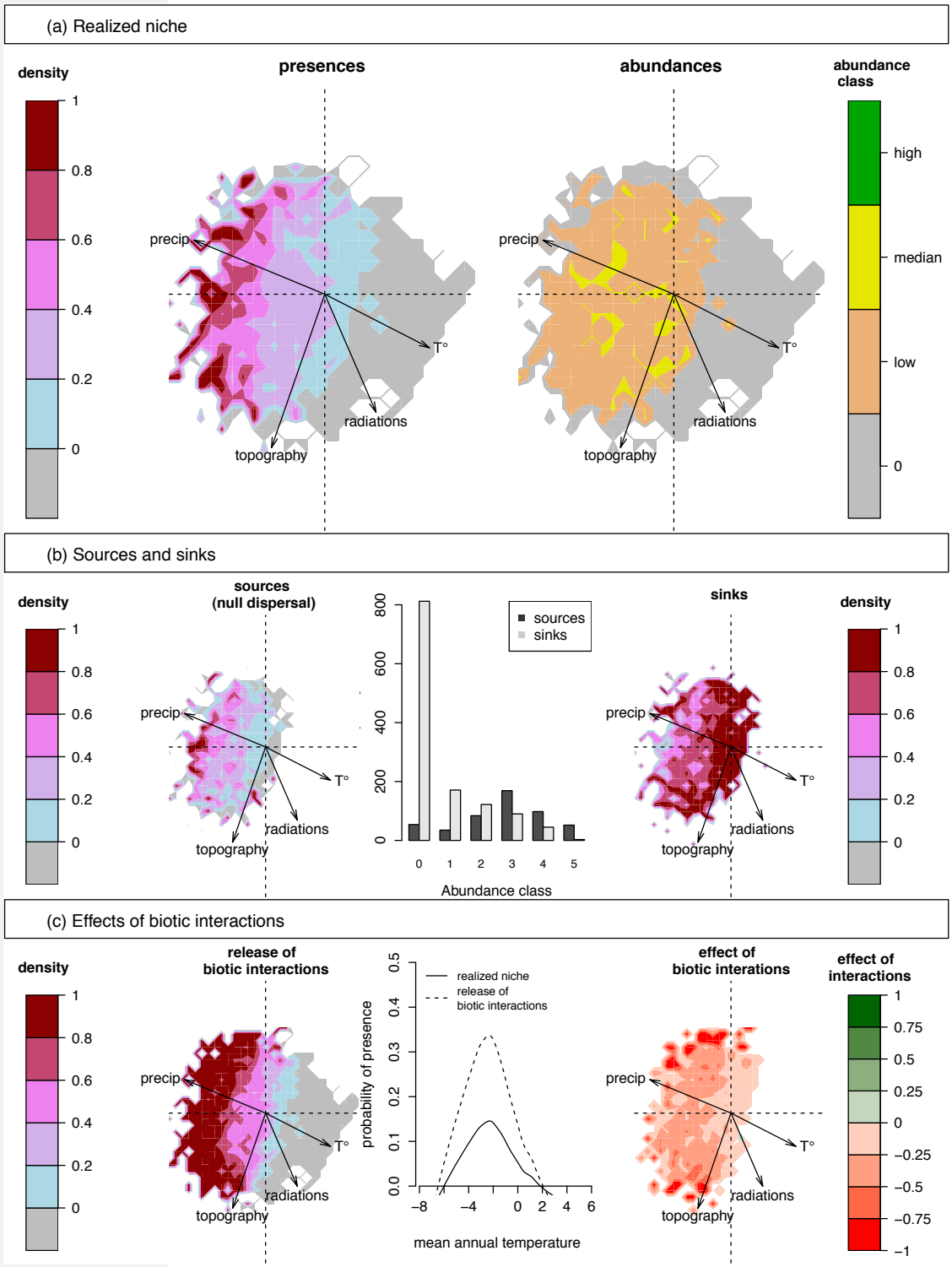
6) Effects of the different drivers on the abiotic niche

Fig. II.S7. Effect of dispersal and biotic interactions on the abiotic niche for 3 other species. **A:** *Dactylis glomerata*. **B:** *Vaccinium myrtillus*. **C:** *Plantago alpina*. The abiotic niche space is represented by the first two axes (53% of inertia) of a PCA of the abiotic variables. **(a)** Realized niche. Predictions of model ABD are presented in this figure. Left: density of predicted presences normalized by the number of sample plots within each grid cell. Right: third quartile of predicted abundance class within each grid cell. Low: <5% cover; Medium: 5% to 25% cover; High:>25% cover. **(b)** Left/right: Proportion of sources/sinks among predicted presences. Middle: abundances in source and sink plots. **(c)** Effect of biotic interactions. Left: density of predicted presences with co-occurrence indices equalling zero, normalized by the number of sample plots within each grid cell. Right: negative and positive effects of the biotic interactions.

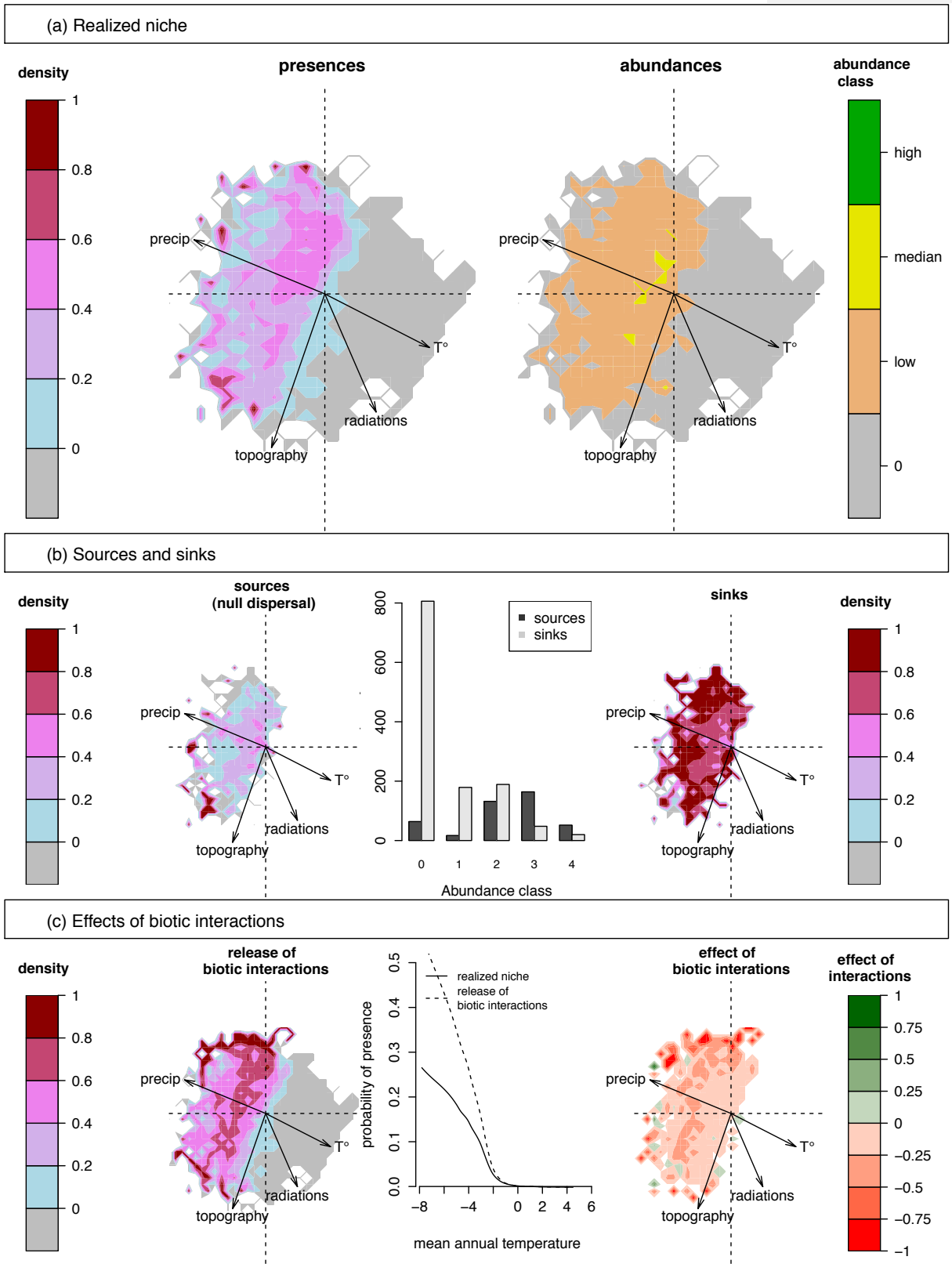
(A) *Dactylis glomerata*



(B) *Vaccinium myrtillus*



(C) *Plantago alpina*



CHAPITRE III:

OPTIMIZING PLANT FUNCTIONAL GROUPS FOR DYNAMIC MODELS OF BIODIVERSITY: AT THE CROSSROADS BETWEEN FUNCTIONAL AND COMMUNITY ECOLOGY

Boulangeat, I., Philippe, P., Abdulhak, S., Douzet, R., Garraud, L., Lavergne Sébastien, Lavorel S., Van Es, J., Vittoz, P., and Thuiller, W. Optimizing plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. *Submitted to Global Change Biology*

Abstract

The pace of on-going climate change calls for reliable plant biodiversity scenarios. Traditional dynamic vegetation models use plant functional types that are summarized to such an extent that they become meaningless for biodiversity scenarios. Hybrid dynamic vegetation models of intermediate complexity (hybrid-DVMs) have recently been developed to address this issue. These models, at the crossroads between phenomenological and process-based models, usually focus on well-chosen plant functional groups (PFGs). The challenge is to build meaningful PFGs that are representative of plant biodiversity, and consistent with the parameters and processes of hybrid-DVMs. Here, we propose and test a framework based on few selected traits to define a limited number of PFGs, which are both representative of the diversity (functional and taxonomic) of the flora in the Ecrins National Park, and adapted to hybrid-DVMs. This new classification scheme, together with recent advances in vegetation modeling, constitutes a step forward for mechanistic biodiversity modeling.

INTRODUCTION

There is compelling evidence of a new biodiversity crisis with species already facing extinction or shifting their geographic ranges and altering their phenology in response to climate change (Bellard *et al.*, 2012, Parmesan, 2006). Effective conservation strategies to counterbalance the effects of environmental change are critical in protecting biological diversity, and need to be supported by sound biodiversity scenarios (Thuiller *et al.*, 2008). This challenge should be met by developing new tools for modeling biodiversity, which involve multiple species and aim to understand and predict changes in biological diversity (e.g. taxonomic or functional diversity). However, despite the efforts of the last ten years, our capacity to predict the impact of environmental changes on biodiversity remains limited (Pereira *et al.*, 2010).

In this context, modeling vegetation is crucial given its pivotal role in determining overall biodiversity and ecosystem functioning. Two different approaches are traditionally used to model vegetation (Thuiller *et al.*, 2008). On one hand, phenomenological models (i.e. habitat distribution models HDMs) can be run on thousands of species, but do not integrate certain key mechanisms (e.g. co-existence and demographic mechanisms), which could hamper their use in biodiversity and ecosystem management at regional scale (Guisan & Thuiller, 2005). On the other hand, process-based models require much more data and knowledge (e.g. LANDIS-II, Scheller *et al.*, 2007), so cannot be applied across large numbers of species. As a consequence, models depicting whole vegetation dynamics over large spatial extents usually involve just a dozen broad plant functional types (PFTs), with insufficient detail to represent plant diversity (e.g. LPJ, Sitch *et al.*, 2003).

Over the last decade hybrid dynamic vegetation models of intermediate complexity (hybrid-DVMs) have been developed. They usually combine existing process-based models with habitat suitability models (Gallien *et al.*, 2010). In order to be run over a large extent, hybrid-DVMs require the modeling entities of intermediate complexity between species level characteristics and broad PFT classifications. These newly defined plant

functional groups (PFGs) should be constructed in relation to the hybrid-DVM sub-models, usually habitat suitability models based on abiotic species niches, and process-based models involving biotic interactions, dispersal, and successional dynamics. Although these mechanisms are explicitly included in hybrid-DVMs, the PFTs available for DVMs are not usually built to model all these ecological mechanisms. For instance, few classifications have used both the species' vegetative properties (representing their dynamic responses to environment) and species' climatic affinity (but see Laurent *et al.*, 2004).

Quite independently of this field of research, functional ecology has always searched for associations between abiotic and biotic environment and species characteristics (Calow, 1987). Significant efforts have been put into building PFTs to predict grassland (e.g. Lavorel *et al.*, 1998) and forest ecosystems (e.g. Verheyen *et al.*, 2003) responses to global changes. These approaches provide a sensible theoretical basis for selecting relevant species characteristics with which to design new PFGs (Lavorel *et al.*, 1997, Pausas & Lavorel, 2003). However, moving from species-level responses to modeling biodiversity dynamics requires the inclusion of species characteristics involved in community assembly mechanisms. For instance, Hérault (2007) proposed an emergent group approach that aimed to both maximize niche differentiation between groups and functional equivalence within groups.

In this paper, we present a framework for building PFGs for hybrid-DVMs to represent vegetation dynamics and ecosystem functioning whilst also depicting biodiversity. We first present the principles of the framework, its features and adaptation to different regional settings. We then apply it to regional flora (National Park in the French Alps) and test its robustness in relation to the aims of biodiversity modeling.

CONCEPTUAL AND METHODOLOGICAL FRAMEWORK

The framework relies on the emergent group approach (Herault, 2007, Lavorel *et al.*, 1997). A set of representative species is classified based on key biological characteristics, to determine groups of species sharing ecological strategies. We divided the framework into four steps (Fig. III.1), presenting the associated concepts and underlying ecological hypotheses for each.

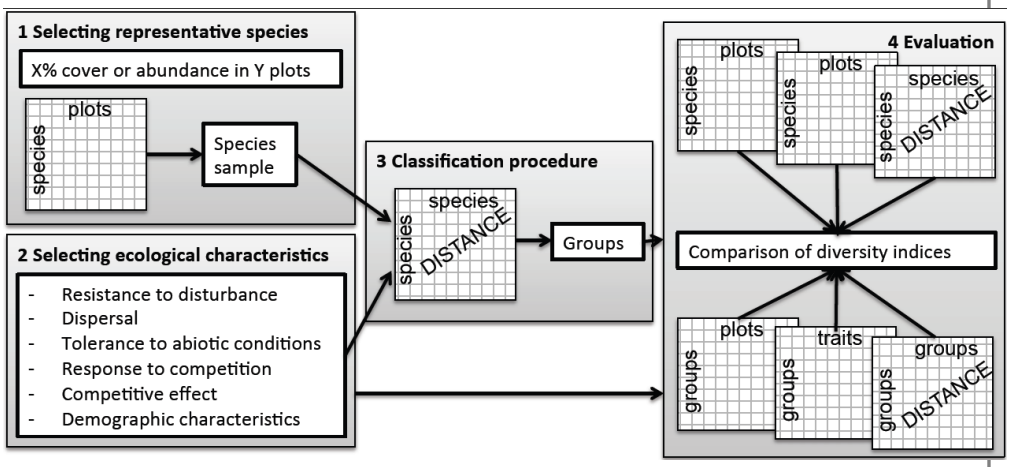


Fig. III.1 Iterative steps to build Plant Functional Groups from a regional flora. The first step is the selection of a subset of the flora which represents the dominant species, relevant to the modeling the vegetation dynamics. The second step is the selection of a limited number of key traits in order to represent the vegetation structure and ecosystem functions but also biodiversity. The third step is a classification to determine emergent groups. The fourth step aims to attribute the groups' trait values and producing diversity indices for the final evaluation.

1 Selecting representative species

Dominant species are usually seen as the main drivers of vegetation dynamics and ecosystem functioning ('Biomass ratio hypothesis', (Grime, 1998). Moreover, according to the well-known species-abundance distribution (Whittaker, 1965), just a few species produce most of the community's biomass. In each vegetation strata (herbaceous, shrub, trees), these species are the most important, not only for structuring the landscape, but also explaining patterns of functional diversity. In order to reduce the number of candidate species for determining PFGs, we propose restricting the classification procedure to these representative species.

Given that hybrid-DVMs may create new situations from those observed locally, the dominance criteria have to account for potential dominance, which can be estimated using the largest possible number of observations of species abundance in communities where the species occurs, even beyond the study area.

2 Selecting ecological characteristics for species classification

The rationale of the approach is to select a minimum set of traits or features which capture the functional divergence between species and the mechanisms modeled in hybrid-DVMs, and combine species-level responses to environmental gradients and mechanisms of community assembly (Fig. III.2).

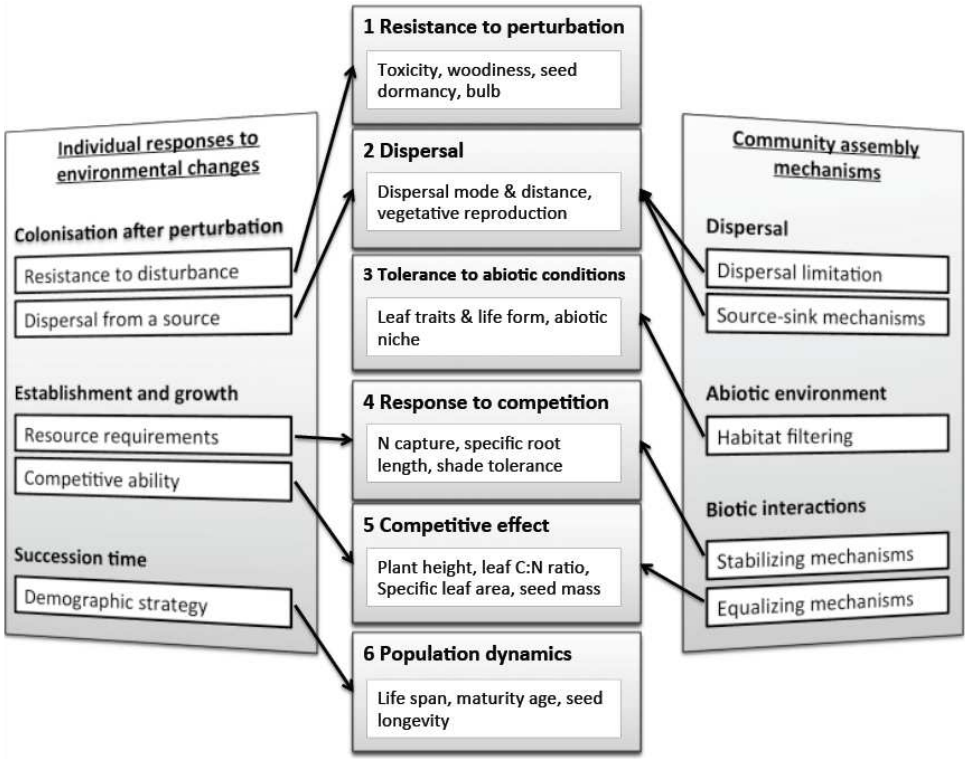


Fig. III.2 The six types of mechanisms for the selection of classification features. Two theoretical frameworks are presented on the sides and are related to the six categories. Left: theoretical background from functional ecology; Right: theoretical background from community ecology; Middle: examples of traits or species characteristics are given for each category.

Functional ecologists have identified the key traits involved in individual plant responses to various environmental disturbances (Cornelissen *et al.*, 2003, McIntyre *et al.*, 1999). Relevant traits are called 'response traits' (Lavorel & Garnier, 2002) and mostly relate to 'vital attributes', which are key life-history characteristics determining the species sequence along vegetation succession (Noble & Slatyer, 1980). They include three groups of traits (Fig. III.2, left). One group relates to plant colonization following disturbance. Two main strategies are considered: either species' persistence during the disturbance (e.g. seed dormancy, defenses against herbivores or fire) or colonization from a source (e.g. dispersal ability, vegetative reproduction). The second group concerns the species' ability to establish and grow, and relates to niche requirements and competitive ability (e.g. plant height or leaf traits) (Fig. III.2, left). The third group

concerns life-history traits influencing species position along ecological successions (e.g. maturity age, longevity) (Fig. III.2, left).

In order to move from species-level responses to community composition and biodiversity, relevant traits must also capture community assembly mechanisms (Suding *et al.*, 2008). In doing so, we directly refer to the coexistence mechanisms implemented in hybrid-DVMs. Three types of mechanisms are commonly distinguished in community assembly theory, namely dispersal, abiotic filtering and biotic interactions (Soberon, 2007) (Fig. III.2, right). Dispersal mechanisms are usually involved in parts of hybrid-DVMs to reflect the spatial dynamics (e.g. dispersal limitation and source-sink mechanisms, Pulliam, 2000) and need to be represented by traits related to species dispersal distances. However, dispersal characteristics, although often considered in functional ecology (Herault, 2007, Pausas *et al.*, 2004), have rarely been included in the PFT classifications available for DVMs. Habitat filtering or the abiotic niche (Guisan & Zimmermann, 2000) is usually derived from habitat suitability models in hybrid-DVMs (e.g. Keith *et al.*, 2008, Midgley *et al.*, 2010). Although climate tolerance is closely related to some vegetative traits (e.g. leaf size, leaf phenology, life form) (Harrison *et al.*, 2010), PFGs need to explicitly merge species with similar abiotic niches, which account for the main abiotic forces of the ecosystem studied (e.g. climatic and soil variables). Finally, the main advantage of hybrid-DVMs is their ability to model biotic interactions. For instance, competition for light is often modeled (e.g. TreeMig, (Lischke *et al.*, 2006), LAMOS, (Cousins *et al.*, 2003)). More generally speaking, competition for resources involves two mechanisms (Chesson, 2000a). Firstly, the equalizing mechanism implies a hierarchy of species according to their competitive effect (e.g. efficiency in resource capture) and results in the dominance of the best competitor. Secondly, the stabilizing mechanism counterbalances the established hierarchy though niche differentiation (e.g. in space, time or type of resource) and can be considered as a response to competition. These two mechanisms are the basis for maintaining species diversity (Chesson, 2000a) and have been shown to contribute to functional diversity (Navas & Violle, 2009).

By combining individual responses to environmental change and community assembly, we have identified six different features that need to be homogeneous within PFGs (Fig. III.2): (1) resistance to disturbance, (2) dispersal, (3) tolerance to abiotic conditions, (4) response to competition, (5) competitive effect, and (6) demographic characteristics.

3 Classification procedure

Once traits and species have been selected, the aim is to reduce the number of modeling entities by defining emergent groups of species (Herault & Honnay, 2007, Lavorel *et al.*, 1997, Pillar, 1999). This issue is usually tackled using a clustering algorithm, for instance agglomerative hierarchical clustering based on a distance matrix (Herault, 2007, Mouchet *et al.*, 2008, Pillar, 1999). If the plant traits are continuous, categorical and/or ordinal, the appropriate measure is the Gower distance, which mixes categorical and quantitative traits (Pavoine *et al.*, 2005, Podani & Schmera, 2006). The agglomerative hierarchical clustering algorithm is based on the distance matrix and provides a dendrogram that is then pruned to form the groups. The choice of the number of groups can be validated using several metrics (Halkidi *et al.*, 2001).

4 Assessing PFGs' ability to represent biodiversity

The aim here is to evaluate how well the PFG delimitation can capture and predict biodiversity patterns using hybrid-DVMs. In addition to taxonomic diversity (TD), functional diversity (FD) is crucial as it directly relates to ecosystem functioning (Hooper *et al.*, 2005). Two FD dimensions could be considered. Firstly, functional divergence (FDiv, Mason *et al.*, 2005) is expected to influence ecosystem processes through complementary resource use (Tilman *et al.*, 1997). Secondly, the functional identity of dominant species has been shown to be the most relevant determinant for some biogeochemical processes (Diaz *et al.*, 2007, Mokany *et al.*, 2008). It can be measured using the community

weighted mean (CWM), which represents the expected trait value for a random community biomass sample (Garnier *et al.*, 2004).

Many elements are simplified for the purposes of clarification, including trait selection and the choice of a limited number of groups. It is therefore important to evaluate the amount of information lost during the process by comparing species-based to PFG-based functional metrics at community level. In other words, if PFG-based functional metrics are able to significantly explain species-based metrics, then the PFG classification is robust and can be used for biodiversity modeling. Species-based and PFG-based diversity measures can be compared using the classification traits, which provide information on the robustness of the clustering, and using independent traits (not used for the classification process) providing cross-validation of the trait selection procedure and testing the robustness of newly built PFGs in capturing the main ecosystem features.

CASE STUDY: FLORA IN THE ECRINS NATIONAL PARK, FRANCE

We applied the PFG construction framework to flora in the Ecrins National Park in order to represent the whole vegetation with limited number of plant functional groups that could be further modeled.

Vegetation database

The Ecrins National Park ('Ecrins' hereafter), in the French Alps (Fig. III.3), is characterized by mountainous to alpine ecosystems (700m to 4000m a.s.l.) and contains over 2000 plant species (Kerguélen, 1993). The National Alpine Botanical Conservatory (CBNA) provided the vegetation-plot database of flora in the surrounding region, including 11,628 community-plots and 1,579 species sampled between 1980 and 2009 (Fig. III.3 and Chapter I). Within each community-plot, species cover (in its strata) was recorded in six classes (1: less than 1%; 2: 1 to 5%; 3: 5 to 25%; 4: 25 to 50%; 5: 50 to 75%; 6: up to 75%) (Braun-Blanquet, 1946). We converted these values to relative abundance using mean cover class percentages.

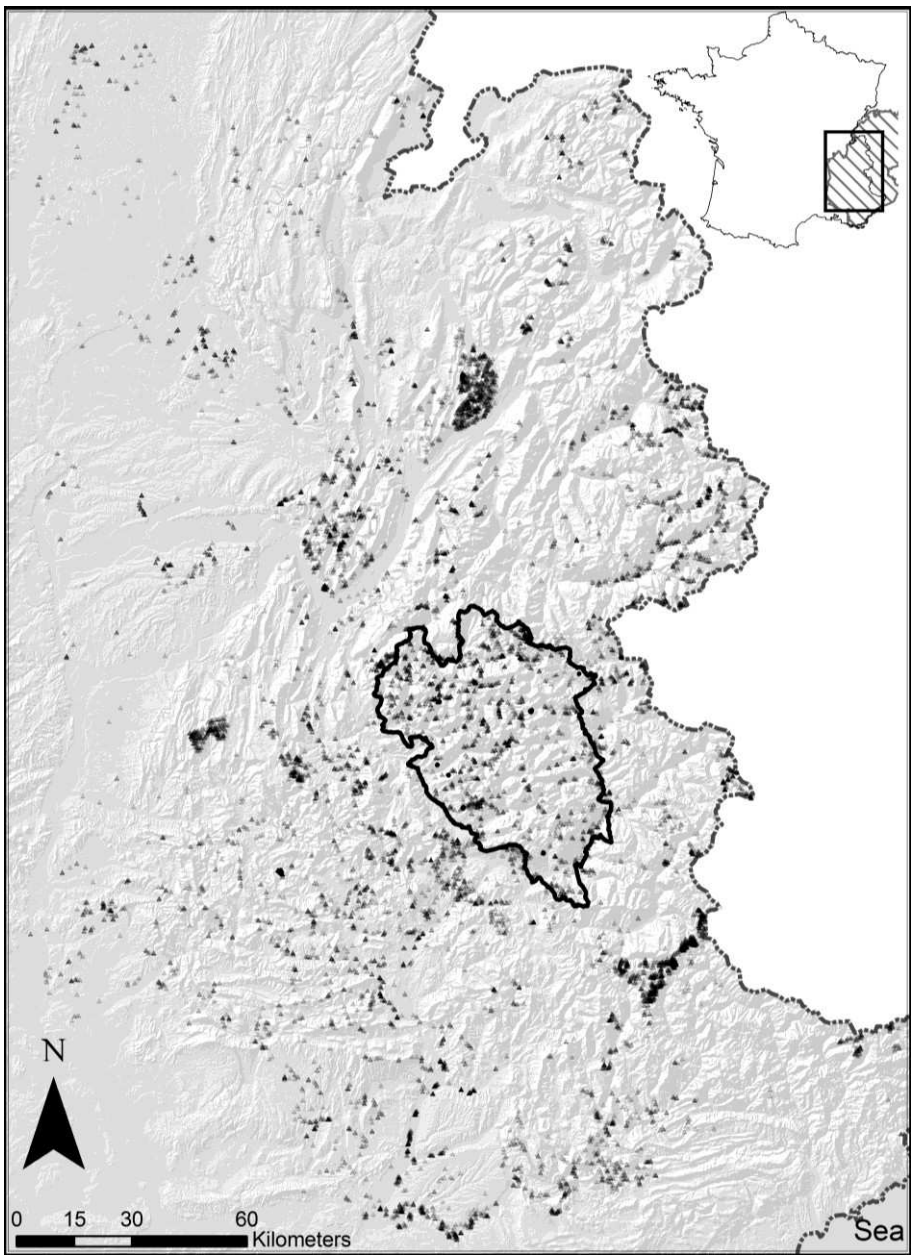


Fig. III.3. Study area. The study area is located in the southeast of France in the French part of the Alpine Arc. Grey strips in the inlay indicate the Alpine Convention area. The Ecrins National Park, delimited with a bold line, is situated along the Italian border, in the southeast of France, close to the Mediterranean Sea. Community plots that have been surveyed in the region are represented by triangles. The hillshade background represents the elevation.

Application of the method

Selecting representative species

We derived species dominance from community plots over the whole region surrounding the Ecrins (11,628 plots) (Fig. III.3). In order to select potential dominant species situated in high productivity plots with multiple strata, we selected species with a cover class above 25% (cover classes 4 to 6) in at least three community-plots. We additionally selected species with maximum relative abundance of over 20% and median relative abundance of over 1% to account for dominant species in low

productivity plots (e.g. scree, sparse grassland). From this pool of dominant species we selected the one with a minimum of 10 observations within the Ecrins. Finally, we retained 412 representative species representing together at least 70% abundance in 80% of the community-plots within the Ecrins.

Selecting ecological characteristics for species classification

Given the limited amount of available data at regional scale, we used a pre-classification based on Raunkiaer's life forms (Raunkiaer, 1934) shown to capture a wide range of plant traits related to ecosystem functioning and ecological succession. For instance, the simple distinction between woody and non-woody species is related to competition, litter decomposition and litter production (Dorrepaal, 2007). As the herbaceous species were mostly hemicryptophytes (261 species), with few geophytes (34 species) and therophytes (17 species), we only distinguished three classes, namely phanerophyte, chamaephyte and herbaceous species. We then chose additional species features to represent the six previously identified categories (Fig. III.2).

1. Resistance to disturbance: In the Ecrins, the main disturbance being grazing by domestic stock, we used a palatability index based on pastoral values (Jouglet, 1999).

2. Dispersal: was represented by distances classes, extracted from Vittoz & Engler (2007) and additional determination following the same protocol. This classification is based on the most efficient dispersal mode, plant height, habitat, seed mass and dispersal attributes (e.g. wings, pappus). It identifies seven classes that discriminate for a log-increase of dispersal distances.

3. Tolerance to abiotic conditions: We conducted a Principal Component Analysis (PCA) on 19 BIOCLIM variables (biologically meaningful variables derived from temperature and rainfall values, see Supporting Information Tab. III.S3) (Hutchinson *et al.*, 2009) at 250m resolution in the Ecrins. Pairwise similarities of species abiotic niches were estimated

from the overlap of their observed distributions (D-metric, Schoener, 1970) projected into the first PCA plan (Broennimann *et al.*, 2011).

4. Response to competition: Because competition for light is commonly modeled (e.g. TreeMig, (Lischke *et al.*, 2006), LAMOS (Cousins *et al.*, 2003)), we chose to depict response to competition by shade tolerance. We used an ecological indicator value for species light requirements (Landolt *et al.*, 2010), adapted to the study region.

5. Competitive effect: Species' competitive ability was represented by plant height, which is involved in competition for light (Westoby *et al.*, 2002) and is also a good proxy for individual biomass (Moles *et al.*, 2009) thus partly including ecosystem productivity (de Bello *et al.*, 2010b).

6. Demographic characteristics: These were considered as broadly included in the pre-classification into life forms representing the main differences in demographic traits such as individual longevity, age at maturity and fecundity (Chapin III *et al.*, 1996, Lavorel & Garnier, 2002, Lavorel *et al.*, 1997). For instance, in our dataset, maturity ages were clearly different for phanerophytes (11.57 +/- 5.68 years), chamaephytes (4.36 +/- 2.48 years) and other species (2.77 +/- 0.80 years).

Classification procedure

For each life form group (phanerophyte, chamaephyte, and herbaceous), we built a distance matrix using Gower's formula (Gower, 1971). Dominant species with missing data were removed, which restricted the set to 290 species representing together at least 70% abundance in 60% of the Ecrins' community-plots. The total pairwise distance between species x and species y was:

$$D(x, y) = (1/5).(|H_x - H_y|/(H_{max}-H_{min}) + |L_x-L_y|/N_L + |D_x-D_y|/N_D + |P_x-P_y|/N_P + (1-O(x,y)))$$

where H is plant height (squared-transformed), L light class, D dispersal class (exponentially-transformed), P palatability class, O climatic overlap (Schoener's D metric) and N_t the number of classes for trait t. We used the Unweighted Pair Group Method with Arithmetic Mean clustering

algorithm (UPGMA, Kaufman & Rousseeuw, 1990), as it has been shown to distort the distance matrix less than other methods (Mouchet *et al.*, 2008). We used the Dunn index, the R-squared (Halkidi *et al.*, 2001), the index of Calinski & Harabasz (Calinski & Harabasz, 1974) and the average silhouette (Kaufman & Rousseeuw, 1990) to choose the number of groups.

The classification identified height phanerophyte groups (P1 to P8), six chamaephyte groups (C1 to C6) and ten herbaceous groups (H1 to H10) (see Supporting Information Fig. III.S1 and Tab. III.S1). Phanerophyte groups separated pioneer trees (e.g. *Larix decidua* P4, and *Betula alba* P8) from climax trees for various types of climate (e.g. external alps P5, internal alps P6), intermediate forests (e.g. *Pinus cembra* P1, *Populus tremula* P2) and subordinate trees (e.g. *Acer opalus* P7, *Fraxinus excelsior* P3).

Chamaephyte groups distinguished between shrubs (e.g. *Alnus alnobetula* C4), dwarf shrubs (e.g. *Vaccinium myrtillus* C6, *Calluna vulgaris* C5), cushion plants (e.g. *Silene acaulis* C3) and other chamaephytes (e.g. *Teucrium chamaedrys* C1, *Cerastium uniflorum* C2). Some of these groups were found in mountainous to subalpine ecosystems (C1, C4, C5) and other modeled alpine ecosystems (C2, C3, C6).

Among the ten herbaceous groups, one represented understorey species (*Prenanthes purpurea* H4). Two other groups represented mountainous to subalpine herbaceous, separated by their dispersal abilities either over short (*Cacalia alliariae* H6) or long distances (*Arrhenatherum elatius* H3). Four groups were mostly found in subalpine ecosystems and differed in terms of their dispersal abilities, palatability or climatic preferences (H2, H5, H7, and H10). Finally, three groups formed alpine meadows with different grazing tolerance, ranging from high (e.g. *Nardus stricta* H9, *Festuca quadriflora* H1) to low palatability (*Cirsium spinosissimum* H8).

Assessing PFGs' ability to represent biodiversity

We tested the resulting PFGs' ability to represent plant diversity by comparing species-based measurements (also including rare species originally excluded from the classification procedure) to PFG-based measurements of diversity. Using the representative species associated to each PFG we built PFG communities, with each PFG having cover class equal to the highest cover class of contributing species in each plot, followed by a standardization to estimate the PFGs' relative abundance. Concerning functional diversity, we selected several sets of traits reasonably represented in our database (i.e. involving at least 657 species, see Tab. III.1).

The seven supplementary traits (woodiness, mowing tolerance, dispersal vector, seed mass, leaf area, specific leaf area, and leaf dry matter content) were extracted from the database ANDROSACE (Thuiller *et al.* unpublished, see Supporting Information Tab. III.S3). We attributed trait values to each PFG after removing outlier species (i.e. with mean distances to other species of the group falling outside of the 95% left-handed confidence interval) (see Supporting Information Fig. III.S2 and Tab. III.S2).

We computed different measures of biodiversity at community scale for the 1,902 Ecrins community plots sampled, and for the 1,128 correctly represented (i.e. where PFGs represent at least 70% of plot abundance). First, we computed the Community Weighted Mean (CWM) for plant height and two independent traits (i.e. not used to build PFGs), namely seed mass and mowing tolerance. Secondly, we used Rao Quadratic entropy as a common framework for taxonomic diversity and functional divergence (de Bello *et al.*, 2010a). We computed functional divergence for classification traits and for independent traits. In addition, we computed functional divergence using traits of the LHS scheme of ecological strategies, as proposed by Westoby (1998), since they are intended to represent the main inter-specific differences in ecological strategies.

Species-based diversity measure	PFG-based diversity measure	Correlation N=1902 plots	Correlation N=1128 plots	Number of species
Classification traits				
CWM_H	CWM_H	0.96	0,99	959
FD_c	FD_C	0.77	0,90	982
Independent traits				
CWM_M	CWM_M	0.65	0,74	974
CWM_S	CWM_S	0.55	0,62	657
FD_I	FD_I	0.55	0,71	963
FD_{LHS}	FD_{LHS}	0.68	0,75	647
TD	TD	0.52	0,76	1579

Tab III.1 Correlations between species-based and PFG-based diversity metrics. The number of species involved in the comparison varies according to the availability of trait data. N=1,902 plots corresponds to all community-plots in the Ecrins National Park. N=1,128 plots corresponds to the well-represented plots, where dominant species represent at least 70% of the abundance. Three different Community Weighted Means are computed for plant height (CWM_H), mowing tolerance (CWM_M) and seed mass (CWM_S). Three different functional divergence measures are proposed, with varying trait combinations. FD_c (classification traits): plant height, Raunkiaer life form, and dispersal distance class.FD_I (independent traits): Mowing tolerance, woodiness, dispersal vector, and seed mass. FD_{LHS}: plant height, seed mass, leaf traits (Leaf area, Specific Leaf Area, Leaf Dry Matter Content). TD is a measure of taxonomic diversity (Simpson index).

Generally speaking, we observed strong correlations between species-based and PFG-based indices, which suggest that the main biodiversity patterns are adequately captured by our PFG classification (Tab. III.1 and Fig. III.4). Note that both functional identity (CWM) and functional divergence (FDiv) are preserved after the reduction of the overall vegetation to 24 PFGs. For classification traits, functional diversity indices (CWM_H and $FDiv_C$) there was a significant correlation between species-based and PFG-based implementations (Tab. III.1), proving that there was a sufficient number of groups to represent the properties of the vegetation. Correlations for indices involving independent traits (CWM_M, CWM_S, and $FDiv_I$) were also strong and demonstrated that the few selected species characteristics were capable of capturing trait syndromes. Moreover, the functional divergence of the LHS scheme ($FDiv_{LHS}$) was well captured, showing that the main plant strategies were comprehensively summarized by the 24 PFGs. However, the associated graph showed that plots with low $FDiv_{LHS}$ were not well classified (Fig. III.4d). The robustness of the classification was also illustrated by the limited impact of missing data and thus of dominant species. With only 70% of the species identified as representative (290 out of 412), the main diversity trends were preserved, even taking into account plots with missing representative species (Tab. III.1). Finally, although designed to represent functional diversity, the PFGs also captured much taxonomic diversity, in particular when all the dominant species from all plots were represented (Pearson correlation = 0.76, Tab. III.1).

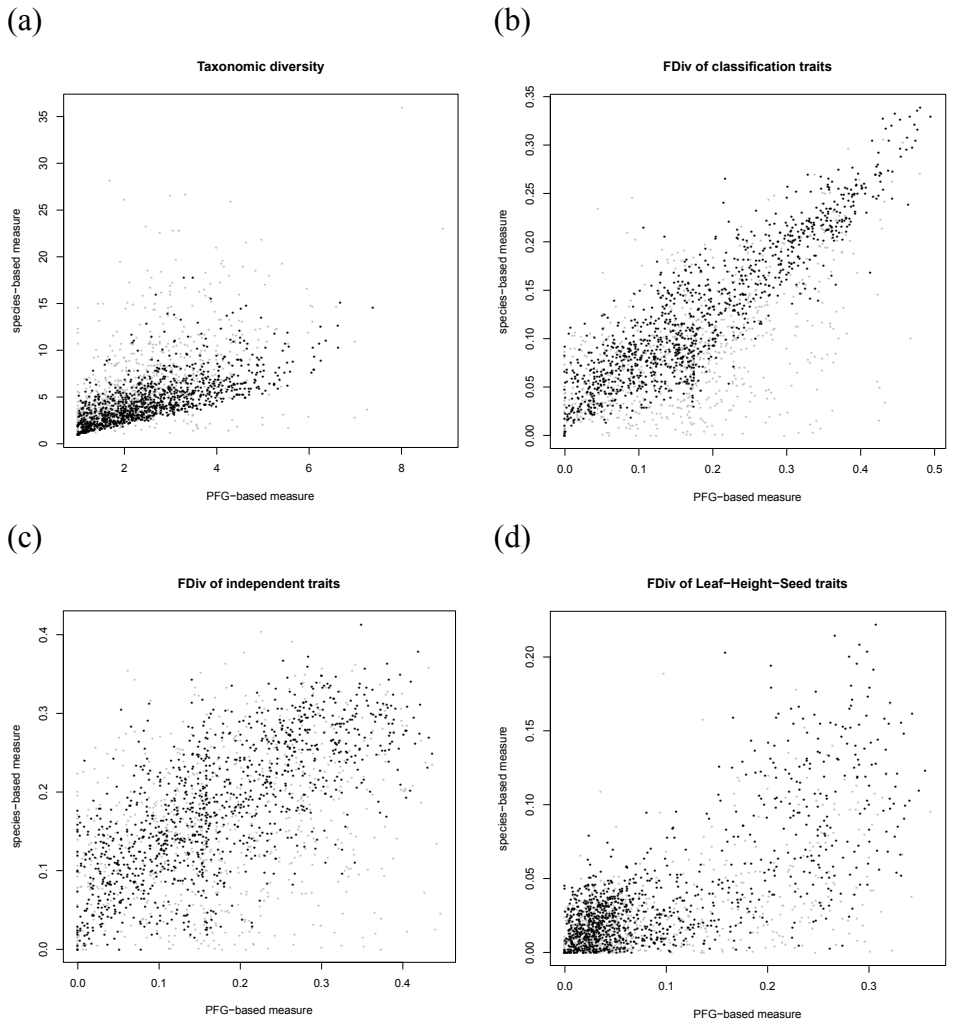


Fig. III.4. Comparisons of species-based and PFG-based measurements of diversity. The following graphs show the relationship between species-based and PFG-based measurements of diversity. Results for all 1,902 plots are shown as grey dots and results for the 1,128 well-represented plots are shown as black dots. Four different indices are presented. **(a)** Taxonomic diversity. **(b)** Functional diversity of classification traits, including plant height, Raunkiaer life form, and dispersal distance class. **(c)** Functional diversity of independent traits, including mowing tolerance, woodiness, dispersal vector, and seed mass. **(d)** Functional diversity of Leaf-Height-Seed traits, including plant height, seed mass and three leaf traits (Leaf area, Specific Leaf Area, Leaf Dry Matter Content).

DISCUSSION

A comprehensive framework for the selection of key classification features

Previous studies have highlighted the need to move from life form based classification to emergent group classification (Epstein *et al.*, 2001, Kattge *et al.*, 2011). Here, we propose a framework to include the minimum set of relevant traits with which PFG can be modeled and overall plant diversity represented. In our example, the selected traits made it possible to use PFGs in hybrid-DVMs because they represent the main mechanisms of these models (competition for resources, tolerance to abiotic conditions, and dispersal). Furthermore, they can depict functional identity and divergence in species assemblages, which makes them suitable for assessing biodiversity. The main limitation to including

more species and improving trait selection remains data availability, although considerable efforts have been made to compile global plant trait databases (Kattge *et al.*, 2011).

Representing diversity using a limited number of entities

The comparison between species-based and PFG-based functional diversity indices shows that although some information is lost, the variation of functional diversity between plots remains similar (Tab. III.1). Previous studies have already showed that CWM is well described even when only the species that produce the largest proportion of the biomass are used (Garnier *et al.*, 2004, Pakeman & Quested, 2007) because these species are expected to be the determinant of ecosystem properties (Grime, 1998). Concerning taxonomic diversity, the biomass ratio hypothesis suggests that dominant species are structuring the communities, and may facilitate the establishment of subordinate species (Grime, 1998). A strong association may therefore exist between dominant and subordinate species, allowing dominant species to reflect the diversity of the entire community. However, ignoring less abundant species might make it difficult to represent the dynamics of the vegetation in certain situations. For instance, some very special habitats such as scree slopes, or peat bogs with mostly rare species might be poorly modeled.

Classifying species into groups is justified by functional redundancy (Walker, 1992) but although we assumed that dominant species represent all the relevant characteristics of the vegetation and that emergent groups are clearly distinct, it is more likely that species are positioned along a functional continuum (Westoby *et al.*, 2002). Therefore, some species may have characteristics that are shared by several groups or continuous traits that overlap between two groups. New methods need to be developed in order to optimize the number of groups. For instance, they could include fuzzy classification methods (e.g. Pillar & Sosinski, 2003) and optimize correlations of functional diversity measures (with species-level based measures) in addition to traditional indices measuring homogeneity within, and heterogeneity between groups.

Future directions

The validity of plant functional classifications has been tested in the literature using experimental (e.g. Bret-Harte *et al.*, 2008, Keith *et al.*, 2008), empirical (e.g. McIntyre & Lavorel, 2001, Pausas *et al.*, 2004) and theoretical approaches (e.g. Bond *et al.*, 2005, Bradstock *et al.*, 1998). However, neither these studies nor our own account for vegetation dynamics. Further work is needed to test the validity of these groups in a dynamic context, for instance retrieving the observed diversity and vegetation structure using a hybrid-DVM. We also suggest that our approach is tested in other regions of the world, in different biomes (Mediterranean, sub-tropical) where different ecological mechanisms are structuring the vegetation (e.g. fires rather than grazing).

ACKNOWLEDGMENTS

The research leading to these results received funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement no. 281422. IB was funded by the French “Agence Nationale de la Recherche” with the project SCION (ANR-08-PEXT-03) and by the European Commission’s FP6 ECOCHANGE project (GOCE-CT-2007-036866). We would also like to thank the Ecrins National Park (especially Cédric Dentant and Richard Bonnet), for their valuable input and insightful comments on our work. Thanks also to Version Original for checking and correcting the English in this article.

SUPPORTING INFORMATION

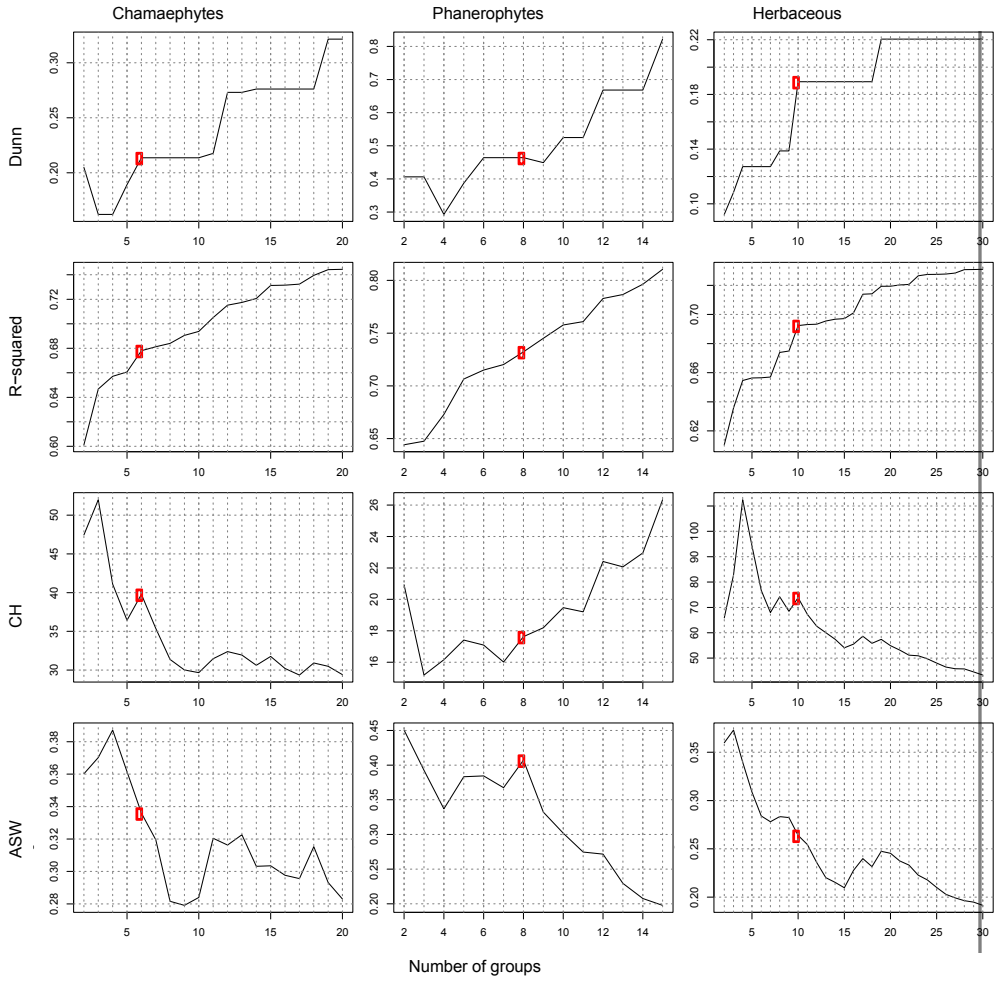
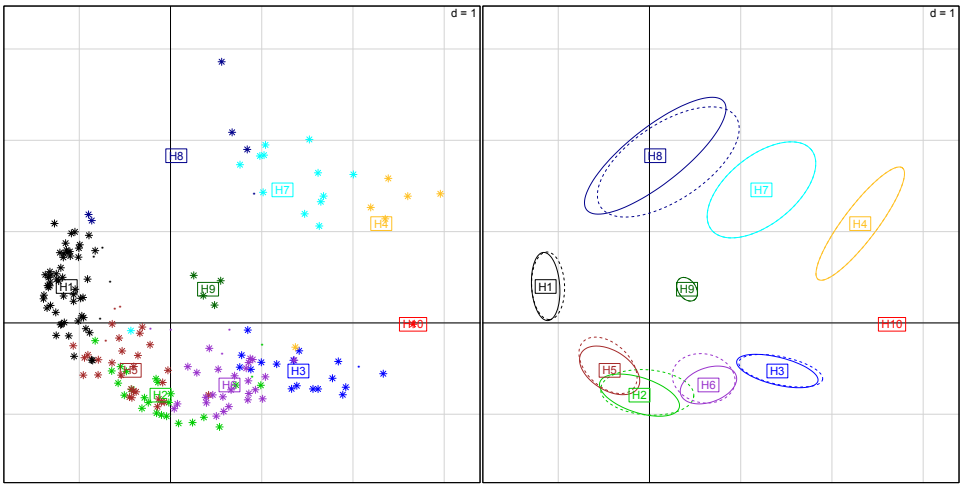
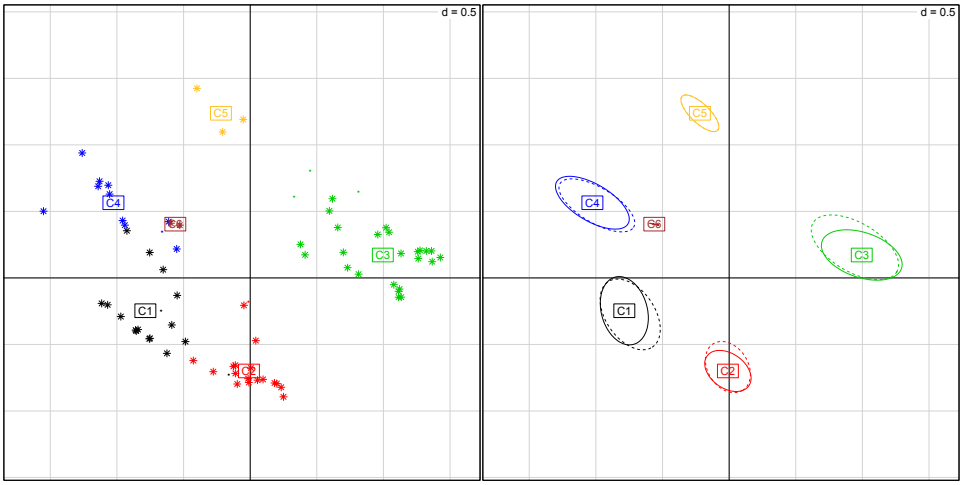


Fig.III. S1 Evaluation of the optimal number of groups. The graphs show, for increasing numbers of groups (x-axis), four evaluation statistics, namely the Dunn index (Dunn), the R-squared, the Calinski & Harabasz index (CH) and the mean silhouette width (ASW). Each column corresponds to a dendrogram and the red circles to the chosen number of groups.

(a)



(b)



(c)

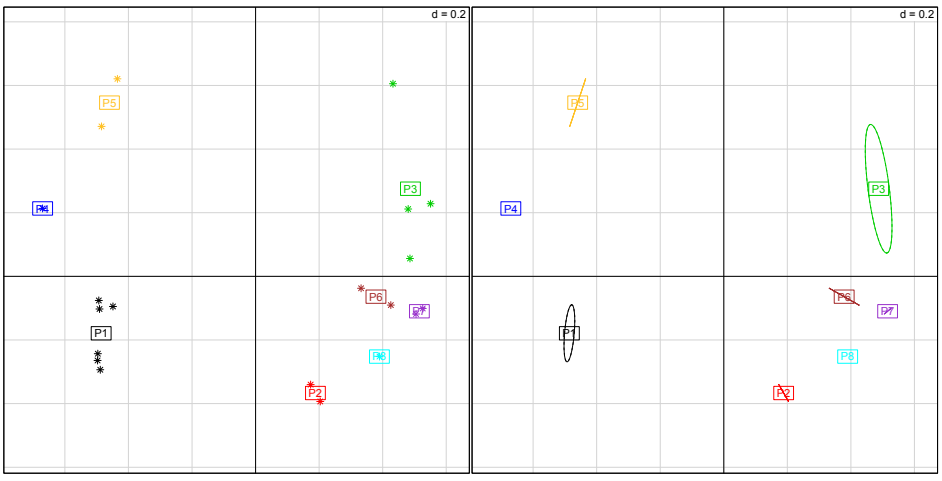


Fig. III.S2. Effect of removing outlier species. The following graphs represent the distance matrices, through a principal coordinate analysis, for (a) Herbaceous, (b) Chamaephytes and (c) Phanerophytes. On the left-hand side, graphs include all species positions. Dots show outlier species. On the right-hand side, we can see the effect of removing outliers on the spread of each group represented by dashed ellipses (all species) and solid line ellipses (core species). The ellipses include two-thirds of the species.

Tab. III.S1 Species in each group. The list of species is given for each group. Outlier species have been removed (i.e. with mean distances to other species of the group falling outside of the 95% left-handed confidence interval).

Group	Species list
H1	*Oxyria digyna, Polygonum viviparum, Ranunculus glacialis, Ranunculus kuepferi, Ranunculus montanus, Geum montanum, Geum reptans, Potentilla aurea, Potentilla erecta, Potentilla grandiflora, Saxifraga stellaris robusta, Linaria alpina alpina, Carex capillaris, Carex curvula, Carex foetida, Carex frigida, Carex nigra, Carex panicea, Carex rupestris, Eriophorum latifolium, Eriophorum polystachion, Eriophorum scheuchzeri, Kobresia myosuroides, Trichophorum cespitosum, Juncus alpinoarticulatus alpinoarticulatus, Juncus trifidus, Luzula alpinopilosa, Agrostis alpina, Agrostis rupestris, Alopecurus alpinus, Avenula versicolor versicolor, Festuca halleri halleri, Festuca quadriflora, Phleum alpinum, Poa alpina, Poa cenisia, Poa laxa, Doronicum grandiflorum, Trisetum distichophyllum, Athamanta cretensis, Hieracium glaciale, Leontodon montanus, Leontodon pyrenaicus helveticus, Taraxacum alpinum, Campanula cochleariifolia, Astragalus alpinus, Lotus alpinus, Trifolium alpinum, Trifolium pallescens, Achillea nana, Gentiana punctata, Arnica montana, Epilobium anagallidifolium, Plantago alpina.*
H2	*Rumex acetosa, Rumex pseudalpinus, Fragaria vesca, Galium aparine, Galium verum, Carex caryophyllea, Carex sempervirens, Agrostis capillaris, Agrostis stolonifera, Festuca nigrescens, Sesleria caerulea, Astrantia major, Leucanthemum vulgare, Carum carvi, Meum athamanticum, Chenopodium bonus-henricus, Lathyrus pratensis, Lotus corniculatus, Onobrychis montana, Trifolium montanum, Trifolium pratense, Geranium sylvaticum, Plantago media.*
H3	*Ranunculus acris, Trollius europaeus, Urtica dioica, Aegopodium podagraria, Anthoxanthum odoratum, Arrhenatherum elatius elatius, Dactylis glomerata, Deschampsia cespitosa, Festuca rubra, Crepis pyrenaica, Poa pratensis, Taraxacum officinale, Heracleum sphondylium, Pimpinella major, Trifolium repens, Vicia cracca, Plantago lanceolata.*
H4	*Aconitum lycoctonum vulparia, Aruncus dioicus, Dryopteris dilatata, Dryopteris filix-mas, Athyrium filix-femina, Prenanthes purpurea.*
H5	*Pulsatilla alpina, Ranunculus bulbosus, Anthericum liliago, Luzula sieberi, Achnatherum calamagrostis, Agrostis agrostiflora, Briza media, Bromus erectus, Deschampsia flexuosa, Festuca acuminata, Festuca flavescens, Festuca laevigata, Festuca marginata gallica, Koeleria vallesiana, Phleum alpinum rhaeticum, Stipa eriocaulis eriocaulis, Trisetum flavescens, Leontodon autumnalis, Leontodon hispidus, Tolpis staticifolia, Festuca melanopsis, Hugueninia tanacetifolia, Laserpitium halleri, Laserpitium siler, Silene flos-jovis, Hypericum maculatum, Salvia pratensis, Epilobium dodonaei fleischeri.*
H6	*Ranunculus aduncus, Cacalia alliariae, Saxifraga rotundifolia, Valeriana officinalis, Carex flacca, Cicerbita alpina, Luzula nivea, Avenula pubescens, Brachypodium rupestre, Calamagrostis varia, Festuca altissima, Melica nutans, Milium effusum, Molinia caerulea arundinacea, Poa nemoralis, Hieracium murorum, Hieracium prenanthoides, Senecio ovatus ovatus, Chaerophyllum aureum, Chaerophyllum villarsii, Cardamine pentaphyllos, Laserpitium latifolium, Knautia dipsacifolia, Mercurialis perennis, Gentiana lutea, Epilobium angustifolium.*
H7	*Cacalia alpina, Cryptogramma crispa, Asplenium ramosum, Asplenium septentrionale septentrionale, Asplenium trichomanes quadrivalens, Equisetum arvense, Cystopteris fragilis, Gymnocarpium robertianum, Woodsia alpina, Hieracium pilosella, Homogyne alpina, Petasites albus, Tussilago farfara.*
H8	*Cacalia leucophylla, Cirsium spinosissimum, Omalotheca supina, Murbeckiella pinnatifida pinnatifida, Gentiana alpina.*
H9	*Anthoxanthum odoratum nipponicum, Nardus stricta, Poa supina, Silene vulgaris prostrata.*
H10	*Heracleum sphondylium elegans.*

Group	Species list
C1	*Rumex acetosella, Cotoneaster integerrimus, Potentilla neumanniana, Rubus idaeus, Rubus saxatilis, Valeriana montana, Lonicera caerulea, Helianthemum grandiflorum, Helianthemum nummularium, Anthyllis montana, Hippocrepis comosa, Achillea millefolium, Stachys recta, Teucrium chamaedrys, Thymus pulegioides.*
C2	*Rumex scutatus, Salix hastata, Saxifraga aizoides, Saxifraga oppositifolia, Helictotrichon sedenense sedenense, Leucanthemopsis alpina, Cerastium alpinum, Cerastium cerastoides, Cerastium latifolium, Cerastium pedunculatum, Cerastium uniflorum, Sempervivum arachnoideum, Vaccinium uliginosum microphyllum, Antennaria dioica, Thymus polytrichus, Artemisia umbelliformis eriantha, Artemisia umbelliformis umbelliformis.*
C3	*Androsace pubescens, Androsace vitaliana, Primula hirsuta, Primula latifolia, Dryas octopetala, Salix herbacea, Salix reticulata, Salix retusa, Saxifraga bryoides, Saxifraga exarata, Eritrichium nanum nanum, Noccaea rotundifolia, Pritzelago alpina alpina, Gypsophila repens, Sagina glabra, Sagina saginoides, Silene acaulis, Silene acaulis bryoides, Sedum album, Sedum alpestre, Sedum dasyphyllum, Empetrum nigrum hermaphroditum, Rhododendron ferrugineum, Globularia cordifolia.*
C4	*Amelanchier ovalis, Crataegus monogyna, Rosa pendulina, Salix laggeri, Juniperus communis, Alnus alnobetula, Lonicera xylosteum, Cornus sanguinea, Corylus avellana, Ribes petraeum.*
C5	*Arctostaphylos uva-ursi crassifolius, Calluna vulgaris, Hippocrepis emerus.*
C6	*Vaccinium myrtillus, Vaccinium vitis-idaea vitis-idaea.*
P1	*Prunus avium, Sorbus aria, Sorbus aucuparia, Sorbus mougeotii, Pinus cembra, Pinus sylvestris.*
P2	*Populus tremula, Salix daphnoides.*
P3	*Tilia platyphyllos, Acer pseudoplatanus Fraxinus excelsior.*
P4	*Larix decidua.*
P5	*Picea abies, Fagus sylvatica.*
P6	*Pinus uncinata, Betula pendula.*
P7	*Acer opalus, Acer campestre campestre.*
P8	*Betula alba.*

Tab. III.S2. The resulting PFGs and their classification trait values. Trait values were attributed to each group using the mean across species for continuous traits and the majority class for ordinal values, after removing outlier species (i.e. with mean distances to other species of the group falling outside of the 95% left-handed confidence interval). The three life forms classes are P=Phanerophytes, C=Chamaephytes, and H=Herbaceous. There are seven dispersal classes with increasing median distance (Short: 0.1-2m; Medium: 40-100m; Long: 400-500m). Light classes increase with decreasing shade tolerance. Plant height is given in cm. Palatability ranges from 0 (not grazed) to 3 (grazed, with high nutritional value). Habitat represents climatic niche in 4 categories. M=mountainous; MS=mountainous/subalpine; S=subalpine; SA=subalpine/alpine.

Group	Growth form	Dispersal distance	Light preference	Height (cm)	Palatability	Habitat
C1	C	Long (6)	Full light (7)	30	3	MS
C2	C	Medium (4)	Full light (8)	18	3	S
C3	C	Short (1)	Full light (8)	9	0	S
C4	C	Long (6)	Any (6)	208	2	MS
C5	C	Long (6)	Any(6)	63	0	MS
C6	C	Long (7)	Any(6)	18	2	S
H1	H	Short (3)	Full light (8)	18	3	SA
H2	H	Long (6)	Full light (7)	40	3	S
H3	H	Long (7)	Full light (7)	55	3	MS
H4	H	Short (3)	Shade (5)	80	0	MS
H5	H	Short (3)	Full light (7)	41	3	S
H6	H	Short (3)	Any(6)	73	3	MS
H7	H	Medium (5)	Any(6)	18	0	S
H8	H	Short (3)	Full light (8)	19	0	SA
H9	H	Long (7)	Full light (8)	18	3	SA
H10	H	Long (7)	Any(6)	100	3	S
P1	P	Long (6)	Any(6)	1117	2	MS
P2	P	Medium (5)	Any(6)	750	2	MS
P3	P	Medium (4)	Shade (4)	1875	2	MS
P4	P	Long (6)	Full light (7)	2500	0	S
P5	P	Long (6)	Shade (4)	2500	2	M
P6	P	Medium (4)	Full light (8)	1650	2	MS
P7	P	Medium (4)	Shade (5)	600	2	M
P8	P	Medium (4)	Full light (7)	800	2	S

Tab III.S3. BIOCLIM description of variables. We used 19 BIOCLIM variables to estimate species abiotic niches and to determine the abiotic niche plan where distributions were compared between two species. These variables are derived from the monthly temperature and rainfall values in order to generate more biologically meaningful variables. They represent annual trends (e.g. mean annual temperature, annual precipitation) seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month, and precipitation in the wet and dry quarters).

BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Databases	References
Field measurements	Choler P (2005) Consistent shifts in Alpine plant traits along a mesotopographical gradient. Arctic, Antartic, and Alpine Research, 37, 444-453.
Field measurements	Albert CH, Thuiller W, Yoccoz NG, Soudant A, Boucher F, Saccone P, Lavorel S (2010) Intraspecific functional variability: extent, structure and sources of variation. Journal of Ecology, 98, 604-613.
Field measurements	Lavorel S, Grigulis K, Lamarque P *et al*. (2011) Using plant functional traits to understand the landscape distribution of multiple ecosystem services. Journal of Ecology, 99, 135-147.
VISTA	Garnier E, Lavorel S, Ansquer P *et al.* (2007) Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. Annals of Botany, 99, 967-985.
LEDA	Knevel IC, Bekker RM, Bakker JP, Kleyer M (2003) Life-history traits of the Northwest European flora: the LEDA database. Journal of Vegetation Science, 14, 611-614.
BiolFlor	Kühn I, Durka W, Klotz S (2004) BiolFlor: a new plant-trait database as a tool for plant invasion ecology. Diversity and Distributions, 10, 363-365.
Flora Indicativa	Landolt E, Bäumler B, Erhardt A *et al*. (2010) Flora indicativa. Ecological indicator values and biological attributes of the flora of Switzerland and the Alp, Berne, Haupt Verlag.

Tab III.S4. Databases used for species traits or characteristics. They all form the database ANDROSACE that compiles trait values from field measurements in the study area and other trait databases containing species from the study area.

CHAPITRE IV:

FATE-H: A SPATIALLY AND TEMPORALLY EXPLICIT HYBRID MODEL FOR PREDICTING THE VEGETATION STRUCTURE AND DIVERSITY AT REGIONAL SCALE.

Boulangeat, I., Georges, D., Dentant, C., Thuiller, W. FATE-H: A spatially and temporally explicit hybrid model for predicting the vegetation structure and diversity at regional scale. *In preparation for Journal of Applied Ecology*

Abstract

1. Forecasting biodiversity at regional scales, and particularly vegetation structure and diversity, is a major challenge of the scientific research, as it is the primary producer providing resources and habitats for most species. However, current approaches are limited. On one hand, phenomenological habitat suitability models, extensively used to forecast changes in species distribution in response to climate and land use change, do not account for any mechanisms and for the temporal and spatial dynamic of species distributions. On the other hand, existing dynamic vegetation models (DVMs) usually involve only few modelling entities (e.g. plant functional types) that are not designed to represent biodiversity but rather coarse vegetation types. Coupling both approaches have been suggested to extend the current limitations.
2. Here, we propose an innovative hybrid-DVM, combining mechanistic and phenomenological sub-models, and allowing simulating the distribution and abundance of more modelling entities than traditional DVMs, with reasonable computing time and data requirement for parameterization. It includes mechanisms of succession, dispersal, disturbances and habitat suitability. We analyse its capability to retrieve the vegetation structure and diversity at a regional scale, in the Ecrins National Park (France), where the extensive vegetation surveys and knowledge allow the comparisons with models outputs.
3. FATE-H shows a very high accuracy in simulating and distinguishing open and closed habitats, but is weaker to estimate the canopy cover of intermediate and non-equilibrium habitats. The difference between observations and predictions is partly explained by slope and the percentage of mineral soil. The canopy cover of non-equilibrium situation such as recently abandoned pastures and mown areas are generally over-predicted.
4. The diversity of habitats, measured by the diversity of height strata, was highly correlated between observations and the model outputs. The functional diversity, measured using two different sets of plant traits (e.g. LHS strategies), was also significantly related to observations.
5. **Synthesis.** We believe that this hybrid vegetation model addresses one of the major challenges of the ecological research: providing more realistic simulations of vegetation dynamics in a context of climate and land use change at a regional scale relevant for biodiversity management and conservation. Using specific-sub models that can be easily parameterised and fined tune depending on the region of interest, it allows simulating not only changes in vegetation distribution but also changes in functional diversity, a key element for ecosystem functioning.

INTRODUCTION

They are now plenty of evidence that vegetation ecosystems are changing as a consequence of climate and land use change, leading to an unprecedented rate of species' loss, landscape modification and ecosystem disruptions (Lawton & May 1995; Bellard *et al.* 2012). In this context, modelling tools play an important role to investigate the effect of various management practices on biodiversity or to forecast the future of the vegetation under climate and land use change scenarios, ultimately helping decision makers to select the best conservation strategy (Thuiller *et al.* 2008; Parmesan *et al.* 2011). Although forecasting changes in biodiversity has become an important field in ecology, models are still insufficiently robust and not predictive enough. Moreover, they are not dedicated to model biodiversity at regional scales (e.g. protected areas) where biodiversity management and conservation takes place (Pereira *et al.* 2010; Bellard *et al.* 2012).

Biodiversity, although originally referring to species richness, encompasses more generally species diversity, the diversity of resources and the structural complexity of the environment (Hamilton *et al.* 2005). The focus on the dominant vegetation is therefore a basis to evaluate biodiversity changes as it structures the environment by creating habitats and resources for other species. Moreover, the plant functional diversity, mostly determined by dominant plant species ("Biomass ratio hypothesis", Grime 1998), can be directly related to ecosystem functioning and ultimately to ecosystem services (de Bello *et al.* 2010b). These two facets of biodiversity, namely habitat diversity and the plant functional diversity are also expected to be correlated with species richness (across trophic levels) at regional to global scale (Kerr & Packer 1997; Kerr, Southwood & Cihlar 2001; Tews *et al.* 2004).

To be of any used in conservation planning, biodiversity forecasts also needs to account for the spatial and temporal dynamics of change due, for instance, to species' migration rates. There is consequently a demand for models explicitly including the temporal and spatial mechanisms of the response of biodiversity to environmental changes (Bellard *et al.* 2012).

This context makes dynamic vegetation models (DVMs) particularly appropriate to be developed and adapted for dynamic biodiversity modelling.

There are a large range of existing DVMs but most of them are designed to simulate vegetation or biome shifts at regional to global scale (e.g. LPJ, Sitch *et al.* 2003). These DVMs, although very promising for predicting changes in broad vegetation types and biogeochemical processes are of little use for biodiversity forecasting at regional scale (Harrison *et al.* 2010). Moreover, restricted by knowledge, data or computing time, they are not detailed enough, particularly concerning herbaceous ecosystems, and their ability to represent biodiversity has never been explicitly tested (Gallien *et al.* 2010). That is why models capable to account for numerous species such as habitat suitability models (Guisan & Thuiller 2005), although they lack dynamic processes, have constituted until now the most prominent approach to forecast trends in biodiversity (Peterson *et al.* 2002; Lawler *et al.* 2009; Thuiller *et al.* 2011).

Interestingly, the last few years have seen the development of DVMs of intermediate complexity usually based on a coupling of existing process-based models such as demographic models with habitat suitability models (Wintle *et al.* 2005; Keith *et al.* 2008; Brook *et al*. 2009; Anderson *et al.* 2009). These models, hereafter called 'hybrid-DVMs', are usually designed to be run over landscape or regional scales and explicitly represent co-existence and/or dispersal mechanisms (e.g. LPJ-GUESS, Hickler *et al.* 2004 ; LAMOS, Albert *et al.* 2008). The inclusion of process-based sub-models allows them to account for vegetation dynamics (e.g. dispersal, biotic interactions, disturbance) and the use of habitat suitability models to account for multiple modelling entities with reasonable simulation times (Gallien *et al.* 2010). These models point the way to predict community composition dynamics and are promising for biodiversity modelling at regional scale such as protected areas. The challenge is that although the level of details they require prevents their use over large number of species and spatial extent, they need to include

a minimum number of modelling entities to be able to represent biodiversity.

Here we present a newly developed hybrid-DVM called “FATE-H”, a spatially and temporally explicit model combining a succession model, a disturbance model, a dispersal model and including habitat suitability information. We show how, with 24 well-chosen plant functional groups (PFGs), it is able to retrieve the vegetation structure and the spatial biodiversity patterns of an entire national park. We first analyse the modelled spatial distribution of open and closed vegetation by comparison against observations. We then analyse the potential missing factors explaining the mismatching between observed and potential distribution at equilibrium. We expect to potentially overestimate tree cover in recently abandoned areas or where local perturbations have not been taken into account (e.g. avalanches). We also test whether the difference between observed and potential vegetation may be related to missing drivers. We then test how the different model outputs can be transformed and used for forecasting biodiversity patterns. To do so, we first compare observed and predicted habitat diversity (measured by vegetation layers’ diversity). Secondly, we relate observed functional diversity patterns (from field observations) to those retrieved from the simulations. We finally discuss the limits and the potential of FATE-H for future applications.

MATERIAL AND METHODS

We tested the ability of FATE-H to simulate the current state of vegetation diversity in the Ecrins National Park (hereafter 'PNE'), which is a national park characterized by mountainous to alpine ecosystems (700m to 4000m a.s.l) with a majority of open habitats (Fig. IV.1). Given that the PNE has been extensively surveyed and the structure of the vegetation (upper layers' abundances) is known for the whole park, it is a perfect situation for calibrating and testing such a hybrid-model.

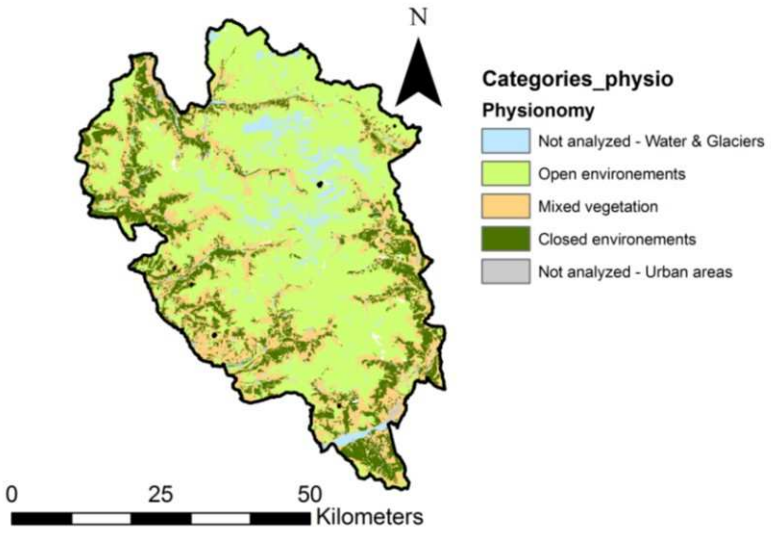


Fig. VI.1 Vegetation physiognomy in the study area. We excluded from the analysis the urban areas, the glaciers and the water, which represent a very small part of the study area. The space in mostly occupied by open areas.

Vegetation database

The available community-plot database of the park contains over 3,000 exhaustive community-plots sampled after 1980 (see chapters I and II). Within each community-plot, species cover was recorded in six classes (1: less than 1%; 2: 1 to 5%; 3: 5 to 25%; 4: 25 to 50%; 5: 50 to 75%; 6: up to 75%) (Braun-Blanquet 1946). We collected functional trait information as well as species characteristics from our field measurements (Choler 2005; Albert *et al.* 2010a; Lavorel *et al.* 2011) and existing databases such as LEDA (Knevel *et al.* 2003), BiolFlor (Kühn, Durka & Klotz 2004), Flora Indicativa (Landolt *et al.* 2010), and VISTA (Garnier *et al.* 2007).

The model FATE-H

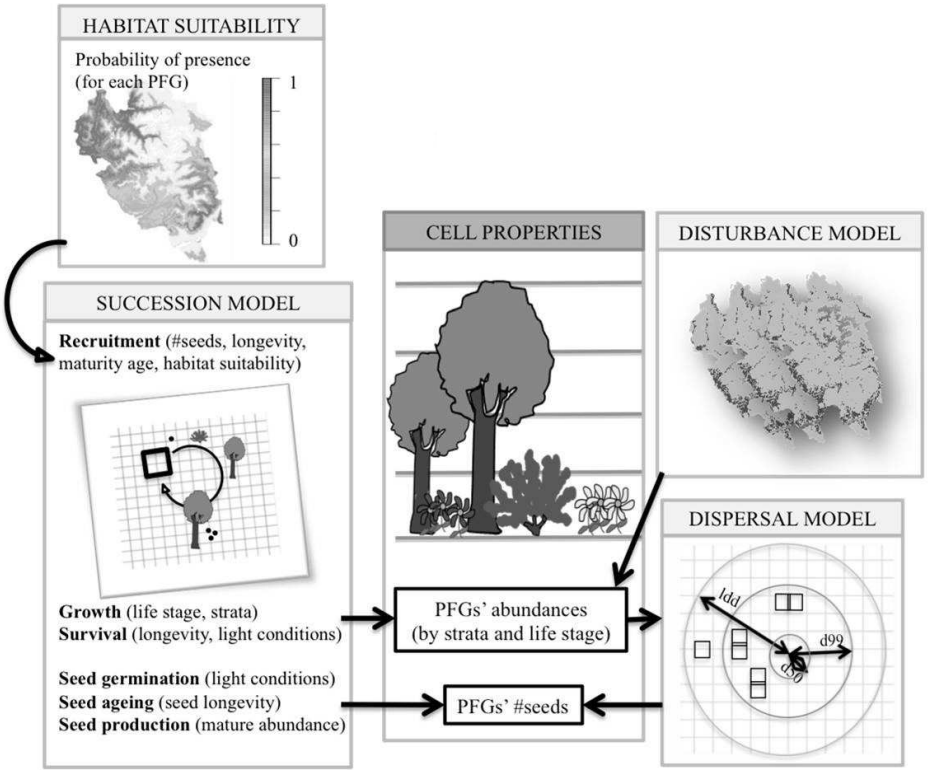


Fig. IV.2 Model FATE-H and its sub-models. The model FATE-H contains four sub-models. The space is divided in grid cells with few main attributes. In each cell, an independent succession model regulates the PFG life cycle. A dispersal model then connects cells though seed dispersal, depending on the abundance of mature plants. Habitat suitability affects the recruitment rate, and disturbances directly modify species abundances. For these two last models, there is no retroaction.

FATE-H simulates the vegetation dynamics resulting from the competitive interactions between modelling entities (e.g. plant functional groups (PFGs) or species), their demography, their dispersal, accounting for habitat/climatic conditions and disturbances. The landscape dynamic is based on a raster grid and modelled through different sub-models (Fig. IV.2). The core sub model is a succession model slightly modified the FATE model proposed by Moore & Noble (1990). The community structure is driven by competition for light at different life stages and demographic traits, combined with a habitat suitability envelope (see Supplementary Information Appendix IV.S1). It describes within-pixel succession dynamic with an annual time step. The habitat suitability only influences the recruitment. Every year, the recruitment of a PFG occurs at a probability given by its probability of presence (i.e. habitat suitability). A place with intermediate habitat suitability (probability around 0.5) is a place where inter-annual variability is high in the model. The second sub-model connects grid cells by a seed dispersal model. The distribution of seeds depends on the dispersal distance with three parameters that defined three circles. In the first circle, 50% of the seeds are distributed uniformly. In the second circle, 49% of the seeds are distributed with the

same concentration as in the first circle but by pairs of pixels, simulating spatial autocorrelation. In the third circle, 1% of the seeds fall into a random pixel, which is very similar to a fat tail distribution in classical kernel functions. The third sub-model is a disturbance model that affects a proportion of each defined age class of each PFG by death or resprouting according to the PFGs characteristics and their tolerance to disturbance.

Defining PFGs

We defined the plant functional groups based on an emergent group approach (Lavorel *et al.* 1997 and chapter III). We selected six characteristics that represent habitat suitability (climatic niche), competition for light (plant height and light niche), dispersal (seed dispersal distance class), demography (Raunkier life forms) and response to grazing (palatability index). Within each life form, we computed pair-wise species distances based on all these features using the Gower metric (Podani *et al.* 1999). We then performed a hierarchical ascendant classification per life form (UPGMA, Podani & Schmera 2006). The number of groups was determined using a selection of 4 indices (Dunn index, average silhouette width, R-squared and Calinski & Harabatz index (1974)) measuring the heterogeneity between groups and/or the homogeneity within groups. We obtained 24 groups that proved to keep most of the information required to estimate vegetation biodiversity such as species richness, taxonomic and functional diversity (see details in chapter III).

Parameterization

General parameters: The model was run over a regular grid at 100m resolution (251,762 pixels) and the vegetation height was divided into five strata (0-1.5m; 1.5-4m; 4-10m; 10-20m; above 20m).

Succession model: Parameters for the succession model were derived from five characteristics, computed as the median or average trait value among representative species of each PFG: the competitive ability for light, estimated by light preference from Landolt *et al.* (2010), the plant

height, the longevity, the maturity age class and Raunkiaer's life form. The full set of parameters for each PFG and calculation details are provided in Supplementary Information (Appendix IV.S2).

Habitat suitability: Habitat suitability was modelled for each PFG using the BIOMOD package in R (Thuiller *et al.* 2009). Species presence-absence representatives of each PFT were pulled together and related to seven environmental variables, namely the slope, the percentage of soil carbon, and five bioclimatic variables (Isothermality, temperature seasonality, temperature annual range, mean temperature of coldest quarter, and annual precipitation, see Hutchinson *et al.* 2009). We used five different statistical models (Generalized Linear Model, Generalized Additive Model, Random Forest, Multivariate Adaptive Regression Splines and Generalized Boosted Models). We performed an ensemble forecasting to combine the binary models outputs of these five models, using weights calculated on the basis of models' predictive accuracy on the test data (Thuiller *et al.* 2009). A detailed description of habitat suitability models is provided in Supplementary Information (Appendix IV.S3).

Dispersal: Dispersal parameters were attributed for all representative species of each group, following Vittoz & Engler (2007) and Engler *et al.* (2009). The median category was then given to the group (see Appendix IV.S2).

Disturbance: Grazing and mowing areas were extracted from the database 'Delphine', which is the result of a complete description and mapping of the environment in the PNE carried out between 1992 and 1998. Three levels of grazing were considered, affecting an increasing proportion of the PFG's abundance in three different age classes (juvenile, mature and senescent) and with two responses, either death or resprouting (Appendix IV.S2). PFG's affected abundances were differentiated according to their average palatability (Jouglet 1999). Mowing disturbance affected 50% of juveniles of all PFGs and 100% of herbaceous mature plants every two years. The PFGs' response to mowing was exclusively resprouting. Whatever the disturbance

considered, juveniles resprouted at age zero, matures at maturity age minus one and senescent plants at maturity age.

Simulations

Simulations started with an empty initial state and ran over 400 years at total. The first 100 years consisted in a seedling time, which allow forests to grow where the environment is suitable, to reach their upper strata and to create shadow for undergrowth. After the seedling, we run 300 years to make sure PFGs distributions were close to equilibrium (Supplementary Information Appendix IV.S4). We analysed the last year of the simulations given the quite steady equilibrium we achieved after seedling (Appendix IV.S4). The stochasticity included in the model (in the habitat suitability model and in the dispersal model) brought very little variability to the final PFGs' distributions (Appendix IV.S4). We therefore presented the results for only one run.

Vegetation structure

We first compared the spatial pattern of the canopy closure (% cover above 1m) with observations using the Cohen's Kappa (κ) for multiple classes. Although it is generally considered as an overly conservative measure of agreement, it is expected to be a more robust measure than simple percent agreement calculation since κ takes into account the agreement occurring by chance (Srijbos *et al.* 2006). Fleiss's equally arbitrary guidelines characterize κ over 0.75 as excellent, 0.40 to 0.75 as fair to good, and below 0.40 as poor. In our case, we did not expect excellent agreement because our model outputs correspond to stable ecosystems whereas the studied area includes transition zones. In order to verify this hypothesis, we specifically looked at the level of canopy closure across seven types of observed vegetation physiognomy (rock, grasslands, moors, 10-40% closing, 40-60% closing, alder forest and forest). We also calculated the difference between observed and predicted cover above one meter and tested whether it was the result of non-equilibrium situations or neglected mechanisms. In order to identify dissimilarities that were persistent through scales, differences between

observations and predictions (predicted minus observed canopy cover) were estimated at incremental scales, each time giving the resulting value to the central pixel, with radius varying from one to ten pixels, and finally averaged (Gaucherel, Alleaume & Hely 2008). We used random forests models to relate the average model disagreement (predicted minus observed) and five potential explanatory variables. These were the percentage of mineral and carbon in the soil representing missing drivers related to soil resources, and slope and aspect as a proxy for missing local disturbances such as avalanches and rock falls. The presence of mowing and grazing at different levels was used to represent different management legacies. Although these variables were either included into the habitat distribution modelling (e.g. soil, slope) or taken into account in the simulation process (e.g. disturbance), we wanted to further test whether they were not sufficiently explicitly accounted for.

Biodiversity assessment

Habitat diversity

We compared the diversity of vegetation strata against observations using the Gini-Simpson index. We considered three different strata according to observations (0-1m; 1-4m; above 4m). For the comparison, we needed to pull together the three upper strata of model outputs. The diversity index was calculated for observations and predictions using relative abundances of each stratum.

Functional diversity

We focussed on a functional divergence measure (FD) that is widely used, the Rao Quadratic entropy (de Bello et al. 2010a). Observed FD was computed using the community plots, which are complete botanical surveys with recorded abundance covers for all species (see Vegetation database). We performed the analysis on 112 selected cells with at least three community plots in which species abundances were averaged. We used two different sets of traits representing different plant strategies. The first set included specific leaf area (SLA), plant height and seed mass, representing the ecological strategies (LHS), proposed by Westoby

(1998). The second was composed of plant height and Raunkiaer's life forms, shown to capture a wide range of plant traits related to ecosystem functioning (Dorrepaal. 2007). To compute simulated functional diversity, we attributed a mean trait to each PFG, according to its representative species, and performed the calculation in all cells.

RESULTATS

Vegetation structure

Using a threshold at 40% of closing, the general comparison between observations and predictions of close and open environments gave a κ equals to 0.58 demonstrating a generally good agreement (see maps, Fig. IV.3). Looking at the results in more details, the predicted percentage of canopy closure across physiognomies types showed that FATE-H succeeded to separate open from closed habitats but had more difficulties to tease apart intermediate habitats (Fig. IV.4). Most distributions of canopy closure among observed classes were bimodal, showing that the model rarely stabilized in situations of intermediate canopy cover, generally associated with non equilibrium situations (between 40 and 60%, Fig. IV.4).

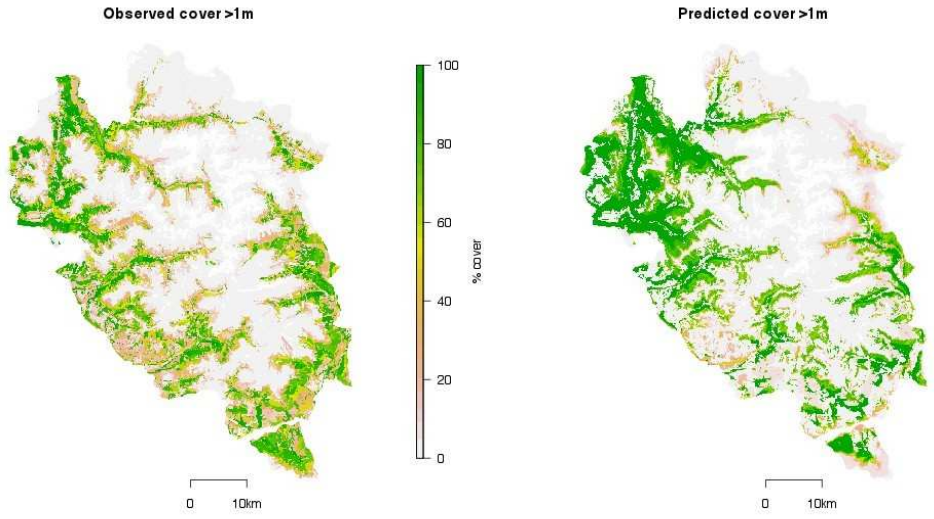


Fig.IV.3 Predicted and observed canopy cover. Canopy cover corresponds to the percentage of cover above 1m. It varies from 0 (open spaces) to 100 (forests). The white background colour indicates not analyzed areas.

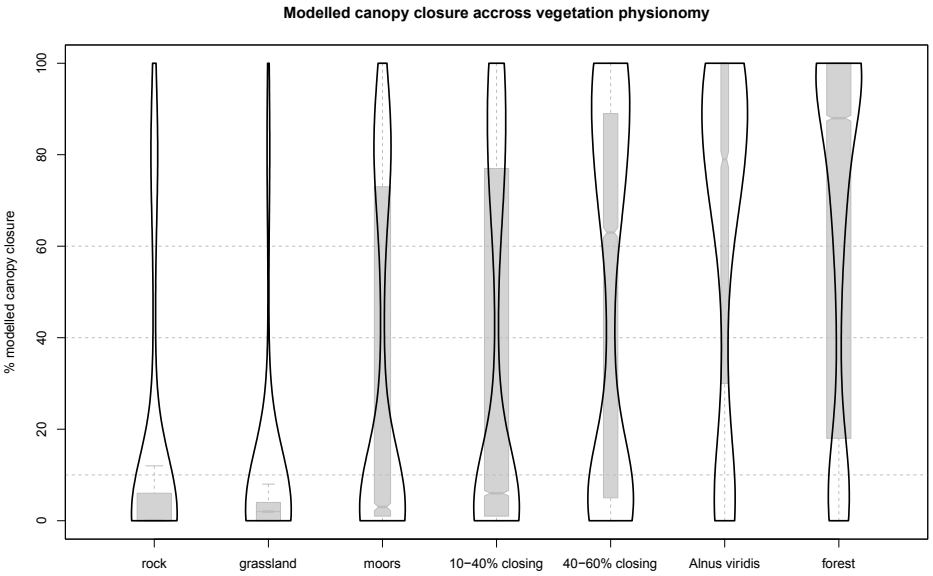


Fig. IV.4 Predicted canopy closure across physiognomy types. The boxplots and the violin plots depict the distribution of predicted canopy cover among analyzed pixels, distinguished into seven physiognomy types. Box plots show extremes values and quartiles. Widths are proportional to the square root of the number of pixels in each class. If the notches for two plots do not overlap then the medians are significantly different at $\alpha = 0.05$.

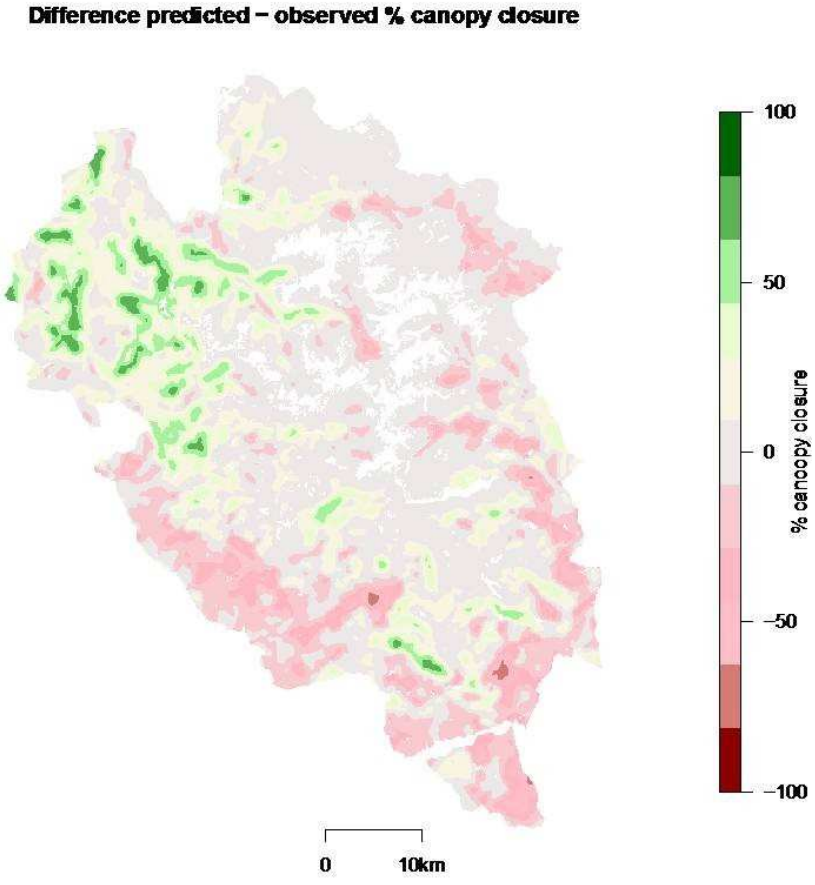


Fig. IV.5 Difference between observed and predicted canopy cover. Negative differences incidate locations where the model predicts less canopy than observed. Positive differences correspond to open space predicted as closed environnements. The white areas has not been analysed.

The differences between observations and model outputs varied in space (Fig. IV.5). The tested variables explained together 35% of this spatial pattern. All variables brought significant explanation with different importance (Tab. IV.1).

Variable	% Increase in MSE
Grazing	98.7
% mineral soil	79.4
Slope angle	61.1
Aspect	55.1
% carbon in the soil	54.2
Mowing	23.7

Tab. IV.1 Variable importance to explain differences between observed and predicted canopy cover. For each variable, models predictions are computed with the randomly permuted variable and the precentage of increase in MSE in given. This is an output of the *randomForest* function in the R package of the same name.

The over-prediction of tree cover was largely explained by slope angle above 30°, where local disturbances such as avalanches or rock falls were the most likely to occur. Areas without grazing were also generally predicted with a larger tree cover (Fig. IV.6), suggesting that they have not yet reached their equilibrium after abandonment. On the contrary, mown areas were predicted with less tree cover than observed (Fig. IV.6), suggesting that simulated effect of mowing was too strong for woody species. Other areas where tree cover was under-predicted were related with little mineral soil, flat terrain and North facing slopes (Fig. IV.6).

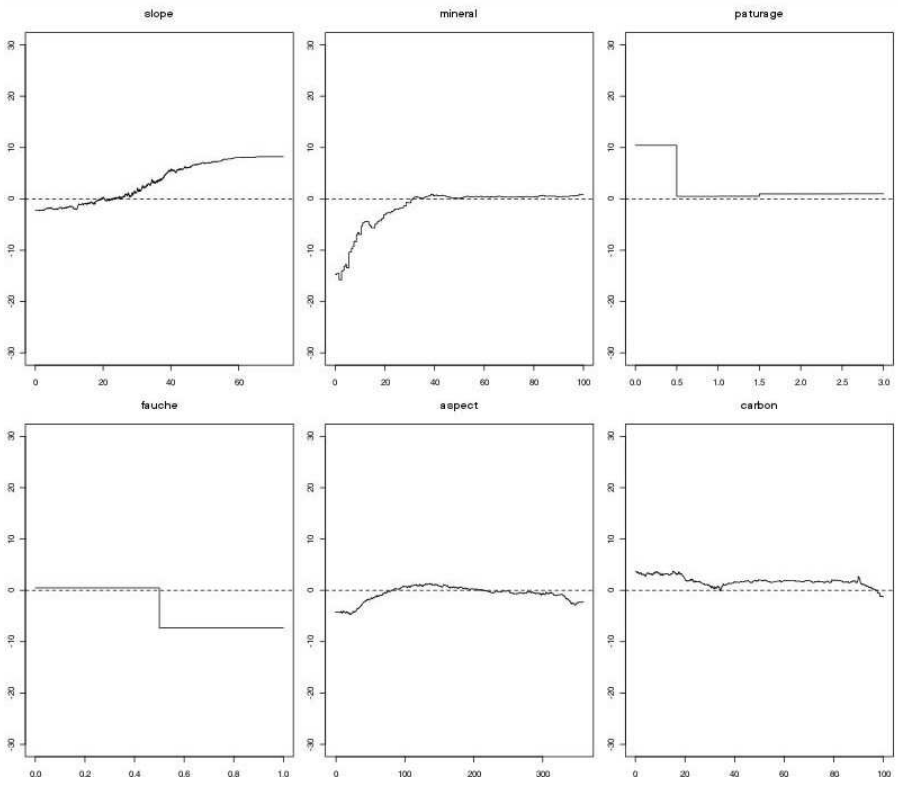


Fig. IV.6 Response curves of the random forest model, to explain the differences between observed and predicted canopy cover. For each variable, predictions are made by keeping constant all other variables (at their mean) and varying the focal explicative variable along its observed range (package R *Biomod*). The final curves give the trend of the effect for

Biodiversity assessment

The simulated diversity of strata was significantly correlated to observations (Pearson correlation = 0.52). However, the model predicted a more heterogeneous pattern of α-diversity than observed (Fig. IV.7).

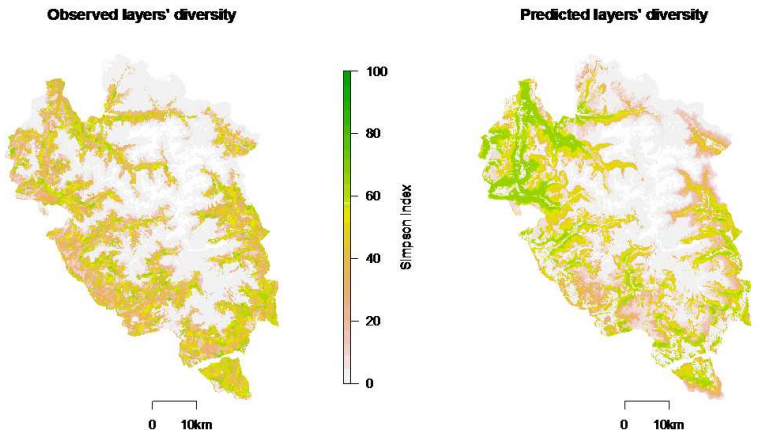


Fig. IV.7 Observed and predicted diversity of habitats. The diversity of predicted and observed strata (below 1m, 1 to 4m, above 4m) has been measured by the Gini-Simpson index. It varies from 0 (low diversity) to 1 (high diversity).

The observed and simulated measures of functional diversity for both ecological strategies (LHS and height and life-forms) showed very high congruence and were significantly correlated (Fig. IV.8). This is interesting, as they were not measured at the same scale. Simulations were carried out at 100m resolution, whereas observed functional diversity were derived from community-plots aggregated at 100m.

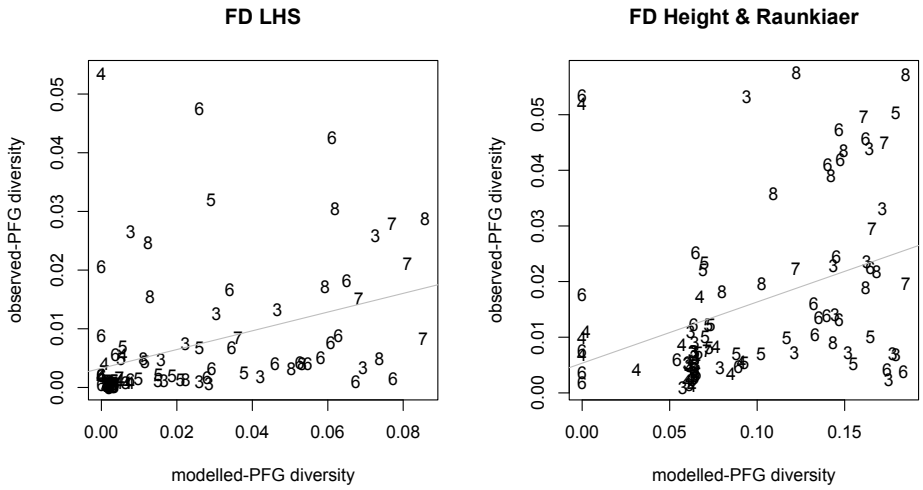


Fig. IV.8 Relationship between observed and predicted functional diversity. The following graphs show the relationship between the measurements of functional diversity based on observations vs predictions. The measures are compared on 112 pixels. The numbers indicates the physiognomy type of the pixel. 3: rocks, 4: grasslands, 5: moors, 6: semi-closed (10-40%), 7: semi-closed (40-60%), 8: forests. Two different sets of traits have been used. (a, left) Three traits have been included: Specific Leaf Area, plant height and seed mass. (b, right) Two species characteristic have been used: Raunkiaer life form and plant height.

Concerning the functional diversity of the LHS schema, which represent the variety of plant strategies in resource use (Westoby 1998), the Pearson correlation was 0.39. The second trait combination, involving

heights and life forms, gave similar results (Pearson correlation = 0.37). In general, the model tended to under-predicted the functional diversity in grasslands, for both trait combinations (Fig.IV.8), suggesting that 10 herbaceous PFG were perhaps not enough to represent the diversity of herbaceous ecosystems.

The predicted pattern of LHS diversity (Fig. IV.9) was highly correlated with the observed habitat diversity (Pearson correlation = 0.91). The Northwest part of the park showed the highest diversity and the centre the lowest. More generally, the diversity increased from the centre, where are found scarce grasslands and approaches to glaciers, to the edges where the environment is less stressful (Figs. IV.7 and IV.9).

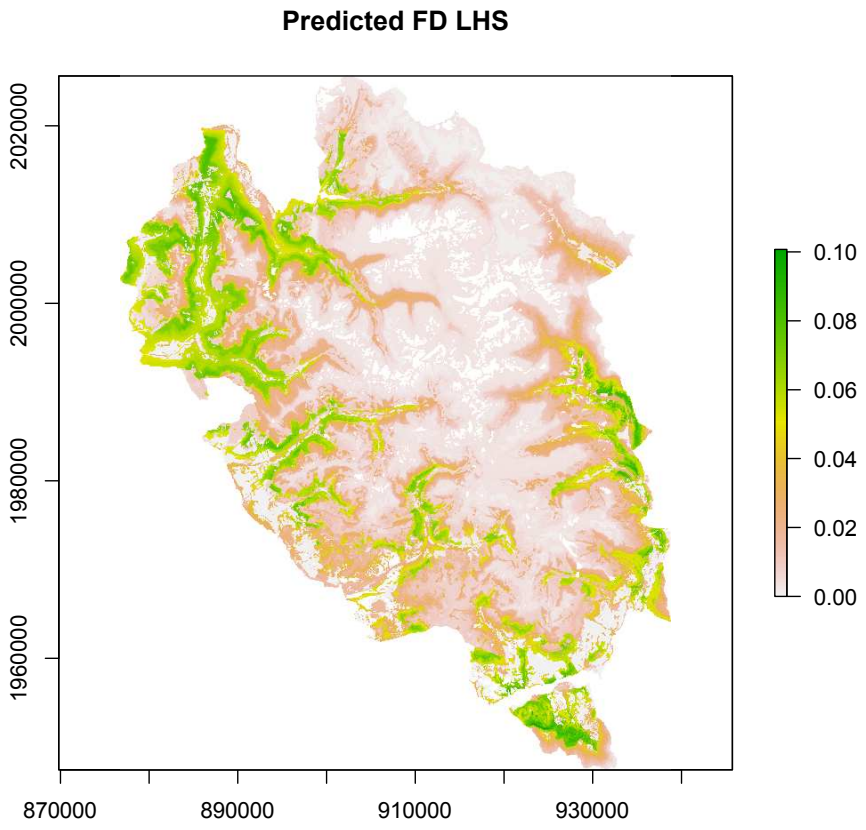


Fig. IV.9 Predicted functional diversity Map. Functional diversity involving LHS traits have been calculated for all pixels using model outputs. It has been measured by the Rao quadratic entropy index.

DISCUSSION

Why using an hybrid-DVM?

The new approach proposed here, relying on combined sub-models at the regional and landscape scales, offers several avenues for predicting biodiversity dynamics.

First, the use of habitat suitability modelling as an input variable and influencing recruitment fulfils the most important assumption of traditional succession model such as FATE, which is the suitability of the study site for the modelled entity. Therefore, the way we accounted for this habitat suitability allows giving some environmental stochasticity in the case of moderate suitability. It is indeed very likely that areas where the habitat suitability of a particular group is difficult to model correspond to places where the PFG dynamic is strongly influenced by other important mechanisms such as competition or dispersal processes. Including both abiotic and biotic conditions in landscape dynamics thereby increases the realism of projections.

Second, FATE-H inherently combines two different study scales. As a first step, habitat-suitability models can be established at the scale relevant for the study area (e.g. regional or global scales). Under these conditions one of the most important assumptions of these models can be fulfilled: pseudo-equilibrium between the plant functional group of interest and the current environment (Guisan & Thuiller 2005). In our example, we included information about climate and soil because we believed they were the most plausible drivers of the large-scale distribution of PFGs. Other important drivers might certainly be included when available (e.g. soil water holding capacity, soil nitrogen). As a second step, the community dynamics modelled by the combination of the succession model together with the dispersal and disturbance models, take place at a level of details appropriated for landscape modelling. The proposed approach appears promising for addressing scaling problems, including limitations of models at each scale (Peters *et al.* 2004). As far as we know, few model combinations have already been implemented in

such a way (Guisan & Thuiller 2005). They are some examples for animal species where landscape models are used as variables for the niche-based models (Wintle *et al.* 2005). Concerning plants, there are very few studies presenting such a combination (for a review see Gallien *et al.* 2010, Franklin 2010). Dullinger *et al.* (2004) carried out a similar analysis by building a spatially explicit model incorporating both climate, biotic interactions and dispersal (see also Albert *et al.* 2008; Williams *et al*. 2008; Smolik *et al.* 2010)

Modeling biodiversity with a hybrid-DVM

To the best of our knowledge, this is one of the first times that a hybrid-DVM is tested empirically to model both the vegetation structure and diversity of an entire region. We demonstrated that FATE-H was able to retrieve the general patterns of the vegetation structure and diversity of the PNE. Using more entities than traditional DGVMs (e.g. LPJ, Sitch *et al.* 2003), and considering not only trees as in Forest Gap Models (e.g. TreeMig, Lischke *et al.* 2006), FATE-H is able to involve a sufficient number of PFGs than can represent the vegetation diversity (see chapter III). In other words, our simulations based on 24 plant functional groups for an entire national park holding more than 1,500 plant species, are able to not only accurately predict the vegetation structure and its distribution but also give insights on the diversity patterns such as functional diversity. These results have some strong implications in terms of biodiversity forecasting. Using such an approach into a protected area would allows to make reliable projections of vegetation diversity patterns, but would also permit to simulate the spatial and temporal response of the vegetation structure and diversity in response to climate and land use change scenarios. It has thus tremendous implications for biodiversity managements in the PNE.

Conceptually, the inclusion of the main coexistence mechanisms into the model and into the PFGs' construction (i.e. abiotic filtering, biotic interactions and dispersal), makes an important step forward in comparison to phenomenological models such as habitat suitability models (Thuiller *et al.* 2008), and should lead to the construction of more

robust forecasts. To give an example, FATE-H simulated the whole dispersal process. The number of dispersed seed depends on the abundance of mature plants that are influenced by the overall community dynamics, and the recruitment depends on the proportion of available seeds and habitat conditions. This is a real progress compared to the simple combination of habitat suitability models and dispersal kernels (e.g. Engler & Guisan 2009, Iverson *et al.* 2006).

Scale considerations and limits

FATE-H, as all DVMs, is clearly limited in precision. It is designed to give intermediate scale trends at regional scales and general patterns only. For instance, it is not made to model within cell heterogeneity, nor to account for biotic interactions between cells, which make the ultimate choice of the resolution decisive for the outcomes precision (see Gallien *et al.* 2010). We also decided to implement a somehow simple dispersal kernel instead of a complicated seed dispersal model. Indeed, the dispersal model needs to remain consistent with the level of details of the whole model and simulation experiment, which is semi-quantitative, with numerous parameters representing more a rank between species rather than continuous values. At this spatial scale (a region) and resolution (100m), we believe it is more important to relate seed dispersal to community dynamics rather than overly complicate the seed dispersal model. Indeed, at 100m resolution, most of plant seeds are expected to fall within the neighboring pixels, while rare long dispersal events are generally highly stochastic and difficult to predict accurately (Kunstler *et al.* 2007). The use of complex kernel functions is therefore limited by the poor available knowledge, is also not consistent with the model scale of details and would increase the simulation time, but would not change the general patterns (results not shown).

Our results suggest that the number of herbaceous PFGs might need to be increased to better represent grassland structure and diversity. The main limitation is the availability of trait data for most of the species. Increasing the number of PFGs with the same dataset would ultimately create some PFGs represented by a single species. In three particular

cases, this is difficult to know whether these groups represent distinct herbaceous types or if they are the result of data uncertainties (e.g. missing data, local error, and extreme field measurement). The number of modeling entities has also to be consistent with the model complexity. For instance, competition for light is not occurring between herbaceous species (no light competition within strata but between strata). This is indeed impossible to parameterize herbaceous competition for light because the model does not account for phenology and we do not know which PFG would grow first in the year, creating shadow for the others. Another challenge for modeling more accurately herbaceous functional groups relates to the resolution and competition for resource. Indeed, coexistence is unlikely to be limited by competition for light in a 100x100m pixel, when only herbaceous species co-occur. Therefore, competition for soil resources is also likely to interplay with competition for light. Unfortunately, information on soil resources such as available nitrogen is lacking over large spatial scale. This lack of competition between herbaceous species could likely explain the under-estimation of certain grasslands diversity.

Missing factors and potential improvements

Subject to available data, the modeling might still be improved. Our results suggest local stochastic disturbances such as avalanches or rock falls might be worth to include in future modeling attempts. It is known that vegetation structure and avalanches do influence each other creating feedback loops (Bebi, Kulakowski & Rixen 2009). The inclusion of a complete avalanche model could turn out to be an improvement in our study area. On the other side, it is very specific to the study area, and would have no general application. Without modifying the present model, it would however be possible to include avalanches as other disturbances, without retroaction. Any other disturbance may be added to the modeling in this way (e.g. fire). As discussed previously, FATE-H lacks mechanisms related to soil resources. It is obvious that coupling FATE-H with a soil water and nitrogen model would complete our approach and open new opportunities to increase the degree of details. On the other hand, it would require more data and will increase

computing time thus reducing the extent of application of the model. More generally, numerous model coupling may be considered, depending on the study area and available data, but it should be consistent with the whole model's degree of details (Gallien *et al.* 2010).

Future applications

In its current form, the model FATE-H can be used in many situations. First, we validated its ability to model biodiversity patterns, which make it possible to build biodiversity scenarios. For instance, it can simulate the future of vegetation structure and diversity in a context of climate change and/or according to various grazing and mowing managements. It can also be used to test the impact of extreme events, at different frequencies and intensities, on the vegetation. Second, it can be used in different ecosystems, regulated by other disturbances (e.g. by fire, Thuiller *et al.* 2007). Finally, it can be used to model the habitat of any species with poor retroaction on the dominant vegetation (Midgley *et al.* 2010). Given that most of the interactions with other organisms have smaller impact than human disturbances and climate on the vegetation, this possibility concerns a large range of animals, and also rare plants.

Ultimate refinements of such an approach will impose to incorporate feedbacks loops. A step forward here would be to incorporate a chain of metapopulation models to simulate the influence of large herbivores (e.g. red deer, chamois and ibex) on the vegetation dynamics together with domestic grazing and climate change. Synergetic impacts and tipping points could then be investigated in relation to different adaptation and mitigation scenarios.

ACKNOWLEDGEMENTS

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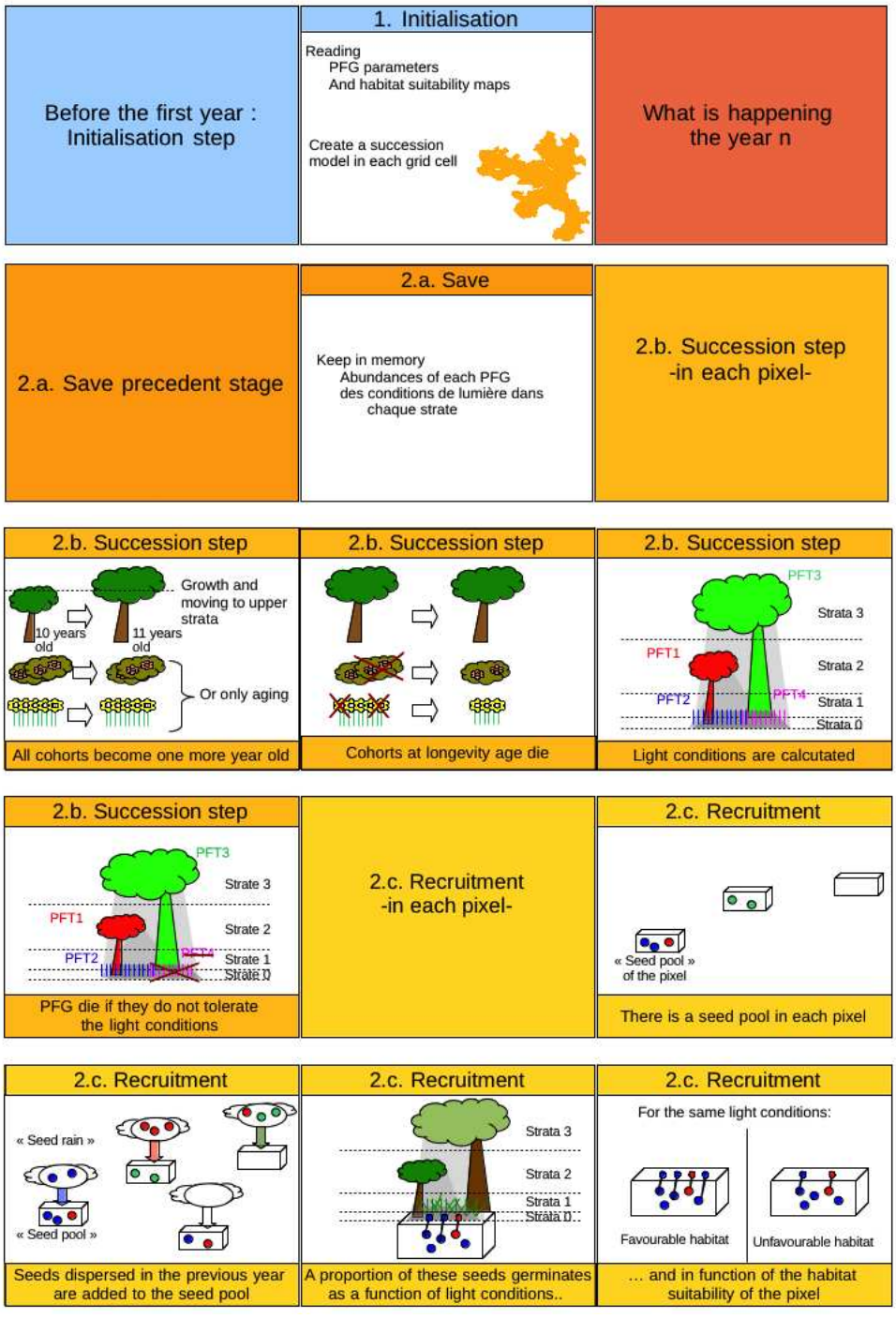
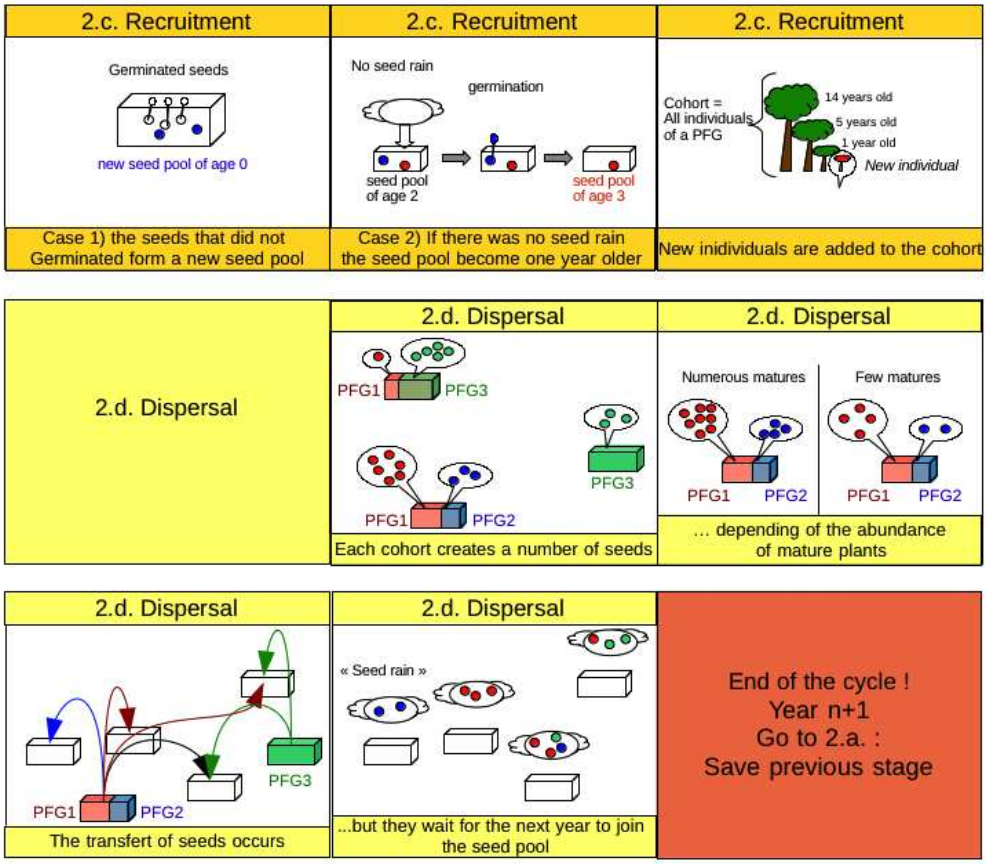
SUPPORTING INFORMATION

APPENDIX VI.S1. DETAILS ON THE MODEL FATE-H




2.c. Recruitment
Germinated seeds
new seed pool of age 0
Case 1) the seeds that did not Germinated form a new seed pool
2.c. Recruitment
No seed rain
germination
seed pool of age 2
seed pool of age 3
Case 2) If there was no seed rain the seed pool become one year older
2.c. Recruitment
Cohort = All individuals of a PFG
14 years old
5 years old
1 year old
New individual
New inidividuals are added to the cohort
2.d. Dispersal
2.d. Dispersal
PFG1
PFG3
PFG3
PFG1
PFG2
Each cohort creates a number of seeds
2.d. Dispersal
Numerous matures
Few matures
PFG1
PFG2
PFG1
PFG2
... depending of the abundance of mature plants
2.d. Dispersal
PFG3
PFG1
PFG2
The transfert of seeds occurs
2.d. Dispersal
« Seed rain »
...but they wait for the next year to join the seed pool
End of the cycle !
Year n+1
Go to 2.a. :
Save previous stage

APPENDIX IV.S2 PFG PARAMETERS

PARAMETERS	PFGs									
	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10
Age of maturity	4	3	3	4	4	4	4	4	4	4
Lifespan	11	10	10	9	9	10	7	9	12	10
Maximum shade	30%	30%	30%	30%	30%	30%	30%	30%	30%	30%
Relative size of immatures vs matures	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %
Strata 1 age threshold	0	0	0	0	0	0	0	0	0	0
Strata 2 age threshold	X	X	X	X	X	X	X	X	X	X
Strata 3 age threshold	X	X	X	X	X	X	X	X	X	X
Strata 4 age threshold	X	X	X	X	X	X	X	X	X	X
Strata 5 age threshold	X	X	X	X	X	X	X	X	X	X
Does PFG disperse everywhere ?	no	no	no	no	no	no	no	no	no	no
Shade active gremination rate	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%
Half-shade active gremination rate	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%
Full-light active gremination rate	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %
Tolerence of Germinant to shade	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tolerence of Germinant to half-shade	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tolerence of Germinant to full-light	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tolerence of Imatures to shade	no	no	no	yes	no	yes	yes	no	no	yes
Tolerence of Imatures to half-shade	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tolerence of Imatures to full-light	yes	yes	yes	no	yes	yes	yes	yes	yes	yes
Tolerence of Matures to shade	no	no	no	yes	no	yes	yes	no	no	yes
Tolerence of Matures to half-shade	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tolerence of Matures to full-light	yes	yes	yes	no	yes	yes	yes	yes	yes	yes
Does mowing kill PFG propagules?	no	no	no	no	no	no	no	no	no	no
Does resonable pasturing kill PFG propagules ?	no	no	no	no	no	no	no	no	no	no
Does quite intensive pasturing kill PFG propagules ?	no	no	no	no	no	no	no	no	no	no
Does high intensive pasturing kill PFG propagules ?	no	no	no	no	no	no	no	no	no	no
First mowing response age treshold	4	3	3	4	4	4	4	4	4	4
Second mowing response age treshold	9	8	8	7	7	8	5	7	10	8
First resonable pasturing response age treshold	4	3	3	4	4	4	4	4	4	4
Second resonable pasturing response age treshold	9	8	8	7	7	8	5	7	10	8
First quite intensive pasturing response age treshold	4	3	3	4	4	4	4	4	4	4
Second quite intensive pasturing response age treshold	9	8	8	7	7	8	5	7	10	8
First high intensive pasturing response age treshold	4	3	3	4	4	4	4	4	4	4
Second high intensive pasturing response age treshold	9	8	8	7	7	8	5	7	10	8
% of first age class mowing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of first age class mowing PFG resprouted	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%
% of second age class mowing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of second age class mowing PFG resprouted	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %
% of third age class mowing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of third age class mowing PFG resprouted	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %
% of first age class resonable pasturing PFG killed	10%	10%	10%	0%	10%	10%	0%	0%	10%	10%
% of first age class resonable pasturing PFG resprouted	50%	50%	50%	0%	50%	50%	0%	0%	50%	50%
% of second age class resonable pasturing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of second age class resonable pasturing PFG resprouted	50%	50%	50%	0%	50%	50%	0%	0%	50%	50%
% of third age class resonable pasturing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of third age class resonable pasturing PFG resprouted	10%	10%	10%	0%	10%	10%	0%	0%	10%	10%
% of first age class quite intensive pasturing PFG killed	50%	50%	50%	0%	50%	50%	0%	0%	50%	50%
% of first age class quite intensive pasturing PFG resprouted	50%	50%	50%	0%	50%	50%	0%	0%	50%	50%
PARAMETERS	PFGs									

	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10
% of second age class quite intensive pasturing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of second age class quite intensive pasturing PFG resprouted	100 %	100 %	100 %	0%	100 %	100 %	0%	0%	100 %	100 %
% of third age class quite intensive pasturing PFG killed	10%	10%	10%	0%	10%	10%	0%	0%	10%	10%
% of third age class quite intensive pasturing PFG resprouted	50%	50%	50%	0%	50%	50%	0%	0%	50%	50%
% of first age class high intensive pasturing PFG killed	90%	90%	90%	0%	90%	90%	0%	0%	90%	90%
% of first age class high intensive pasturing PFG resprouted	10%	10%	10%	0%	10%	10%	0%	0%	10%	10%
% of second age class high intensive pasturing PFG killed	10%	10%	10%	0%	10%	10%	0%	0%	10%	10%
% of second age class high intensive pasturing PFG resprouted	90%	90%	90%	0%	90%	90%	0%	0%	90%	90%
% of third age class high intensive pasturing PFG killed	50%	50%	50%	0%	50%	50%	0%	0%	50%	50%
% of third age class high intensive pasturing PFG resprouted	50%	50%	50%	0%	50%	50%	0%	0%	50%	50%
First age class mowing resprouting age	0	0	0	0	0	0	0	0	0	0
Second age class mowing resprouting age	3	2	2	3	3	3	3	3	3	3
Third age class mowing resprouting age	4	3	3	4	4	4	4	4	4	4
First age class resonable pasturing resprouting age	0	0	0	0	0	0	0	0	0	0
Second age class resonable pasturing resprouting age	3	2	2	3	3	3	3	3	3	3
Third age class resonable pasturing resprouting age	4	3	3	4	4	4	4	4	4	4
First age class quite intensive pasturing resprouting age	0	0	0	0	0	0	0	0	0	0
Second age class quite intensive pasturing resprouting age	3	2	2	3	3	3	3	3	3	3
Third age class quite intensive pasturing resprouting age	4	3	3	4	4	4	4	4	4	4
First age class high intensive pasturing resprouting age	0	0	0	0	0	0	0	0	0	0
Second age class high intensive pasturing resprouting age	3	2	2	3	3	3	3	3	3	3
Third age class high intensive pasturing resprouting age	4	3	3	4	4	4	4	4	4	4
50% of seeds dispersal distance (m)	2	400	500	2	2	2	100	2	500	500
99% of seeds dispersal distance (m)	15	1500	5000	15	15	15	500	15	5000	5000
Long distance dispersal (m)	1000	10000	10000	1000	1000	1000	5000	1000	10000	10000

PARAMETERS	PFGs													
	C1	C2	C3	C4	C5	C6	P1	P2	P3	P4	P5	P6	P7	P8
Age of maturity	5	5	6	11	8	8	17	15	20	15	25	20	15	15
Lifespan	26	20	52	149	46	93	397	178	414	1101	451	161	311	101
Maximum shade	30%	30%	30%	70%	30%	30%	100%	100%	100%	100%	100%	100%	100%	100%
Relative size of immatures vs matures	100%	100%	100%	50%	100%	100%	10%	50%	10%	10%	10%	10%	50%	50%
Strata 1 age threshold	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Strata 2 age threshold	X	X	X	11	X	X	12	3	8	5	8	10	4	3
Strata 3 age threshold	X	X	X	X	X	X	36	9	23	13	21	27	12	8
Strata 4 age threshold	X	X	X	X	X	X	183	X	73	37	61	89	X	X
Strata 5 age threshold	X	X	X	X	X	X	X	X	X	115	191	X	X	X
Does PFG disperse everywhere ?	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Shade active gremination rate	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%
Half-shade active gremination rate	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%
Full-light active gremination rate	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%	90%
Tolerence of Germinant to shade	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tolerence of Germinant to half-shade	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tolerence of Germinant to full-light	yes	yes	yes	yes	yes	yes	yes	yes	no	yes	no	yes	no	yes
Tolerence of Imatures to shade	no	no	no	yes	yes	yes	yes	yes	yes	no	yes	no	yes	no
Tolerence of Imatures to half-shade	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tolerence of Imatures to full-light	yes	yes	yes	yes	yes	yes	yes	yes	no	yes	yes	yes	yes	yes
Tolerence of Matures to shade	no	no	no	yes	yes	yes	yes	yes	yes	no	yes	no	yes	no
Tolerence of Matures to half-shade	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tolerence of Matures to full-light	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Does mowing kill PFG propagules?	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Does resonable pasturing kill PFG propagules ?	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Does quite intensive pasturing kill PFG propagules ?	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Does high intensive pasturing kill PFG propagules ?	no	no	no	no	no	no	no	no	no	no	no	no	no	no
First mowing response age treshold	5	5	6	11	8	8	17	15	20	15	25	20	15	15
Second mowing response age treshold	24	18	50	147	44	91	395	176	412	109	449	159	309	99
First resonable pasturing response age treshold	5	5	6	11	8	8	17	15	20	15	25	20	15	15
Second resonable pasturing response age treshold	24	18	50	147	44	91	395	176	412	109	449	159	309	99
First quite intensive pasturing response age treshold	5	5	6	11	8	8	17	15	20	15	25	20	15	15
Second quite intensive pasturing response age treshold	24	18	50	147	44	91	395	176	412	109	449	159	309	99
First high intensive pasturing response age treshold	5	5	6	11	8	8	17	15	20	15	25	20	15	15
Second high intensive pasturing response age treshold	24	18	50	147	44	91	395	176	412	109	449	159	309	99
% of first age class mowing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of first age class mowing PFG resprouted	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%	50%
% of second age class mowing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of second age class mowing PFG resprouted	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of third age class mowing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of third age class mowing PFG resprouted	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of first age class resonable pasturing PFG killed	10%	10%	0%	10%	0%	10%	10%	10%	10%	0%	10%	10%	10%	10%
% of first age class resonable pasturing PFG resprouted	50%	50%	0%	10%	0%	10%	10%	10%	10%	0%	10%	10%	10%	10%
% of second age class resonable pasturing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of second age class resonable pasturing PFG resprouted	50%	50%	0%	10%	0%	10%	10%	10%	10%	0%	10%	10%	10%	10%
% of third age class resonable pasturing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%

PARAMETERS	PFGs													
	C1	C2	C3	C4	C5	C6	P1	P2	P3	P4	P5	P6	P7	P8
% of third age class resonable pasturing PFG resprouted	10 %	10 %	0%	10 %	0%	10 %	10 %	10 %	10 %	0%	10 %	10 %	10 %	10 %
% of first age class quite intensive pasturing PFG killed	50 %	50 %	0%	10 %	0%	10 %	10 %	10 %	10 %	0%	10 %	10 %	10 %	10 %
% of first age class quite intensive pasturing PFG resprouted	50 %	50 %	0%	50 %	0%	50 %	50 %	50 %	50 %	0%	50 %	50 %	50 %	50 %
% of second age class quite intensive pasturing PFG killed	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of second age class quite intensive pasturing PFG resprouted	100 %	100 %	0%	90 %	0%	90 %	90 %	90 %	90 %	0%	90 %	90 %	90 %	90 %
% of third age class quite intensive pasturing PFG killed	10 %	10 %	0%	10 %	0%	10 %	10 %	10 %	10 %	0%	10 %	10 %	10 %	10 %
% of third age class quite intensive pasturing PFG resprouted	50 %	50 %	0%	50 %	0%	50 %	50 %	50 %	50 %	0%	50 %	50 %	50 %	50 %
% of first age class high intensive pasturing PFG killed	90 %	90 %	0%	50 %	0%	50 %	50 %	50 %	50 %	0%	50 %	50 %	50 %	50 %
% of first age class high intensive pasturing PFG resprouted	10 %	10 %	0%	10 %	0%	10 %	10 %	10 %	10 %	0%	10 %	10 %	10 %	10 %
% of second age class high intensive pasturing PFG killed	10 %	10 %	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% of second age class high intensive pasturing PFG resprouted	90 %	90 %	0%	100 %	0%	100 %	100 %	100 %	100 %	0%	100 %	100 %	100 %	100 %
% of third age class high intensive pasturing PFG killed	50 %	50 %	0%	10 %	0%	10 %	10 %	10 %	10 %	0%	10 %	10 %	10 %	10 %
% of third age class high intensive pasturing PFG resprouted	50 %	50 %	0%	50 %	0%	50 %	50 %	50 %	50 %	0%	50 %	50 %	50 %	50 %
First age class mowing resprouting age	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Second age class mowing resprouting age	4	4	5	10	7	7	16	14	19	14	24	19	14	14
Third age class mowing resprouting age	5	5	6	11	8	8	17	15	20	15	25	20	15	15
First age class resonable pasturing resprouting age	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Second age class resonable pasturing resprouting age	4	4	5	10	7	7	16	14	19	14	24	19	14	14
Third age class resonable pasturing resprouting age	5	5	6	11	8	8	17	15	20	15	25	20	15	15
First age class quite intensive pasturing resprouting age	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Second age class quite intensive pasturing resprouting age	4	4	5	10	7	7	16	14	19	14	24	19	14	14
Third age class quite intensive pasturing resprouting age	5	5	6	11	8	8	17	15	20	15	25	20	15	15
First age class high intensive pasturing resprouting age	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Second age class high intensive pasturing resprouting age	4	4	5	10	7	7	16	14	19	14	24	19	14	14
Third age class high intensive pasturing resprouting age	5	5	6	11	8	8	17	15	20	15	25	20	15	15
50% of seeds dispersal distance (m)	400	40	1	400	400	500	400	100	40	400	400	40	40	40
99% of seeds dispersal distance (m)	1500	150	2	1500	150	500	1500	500	150	150	150	150	150	150
Long distance dispersal (m)	10000	5000	1000	10000	10000	10000	10000	5000	5000	10000	10000	5000	5000	5000

APPENDIX IV.S3 DETAILS ON HABITAT SUITABILITY MODELING

Calibration area:

The calibration was performed in the whole French Alps region. We then projected the models on 'Ecrins National Park' (our study area).

From species occurrences to PFG occurrences:

We considered a PFG as present where at least one of its determining species has been seen. A community where none of its determining species have been seen was considered as a true absence.

Environmental variables:

We used seven environmental variables: the slope, the percentage of carbon in the soil, and 5 BIOCLIM variables (isothermality, temperature seasonality, temperature annual range, mean temperature of coldest quarter and annual precipitation). These variables have been downscaled from a regional climatic model.

BIOMOD parameters:

We used 5 models: Generalized Linear Model (each environmental variables considered as polynomial and stepwise 'best' model selection considering AIC value); Generalized Boosted Models (with a maximum of 3000 trees considered); Generalized Additive Model (with a 4 degree of smoothing of the spline function); Multivariate Adaptive Regression Splines; Random Forest

The prevalence was fixed at 0.5.

We performed 10 repetitions of each run, with a cross-validation (70% of data to calibrate and 30% of data for evaluate the models)

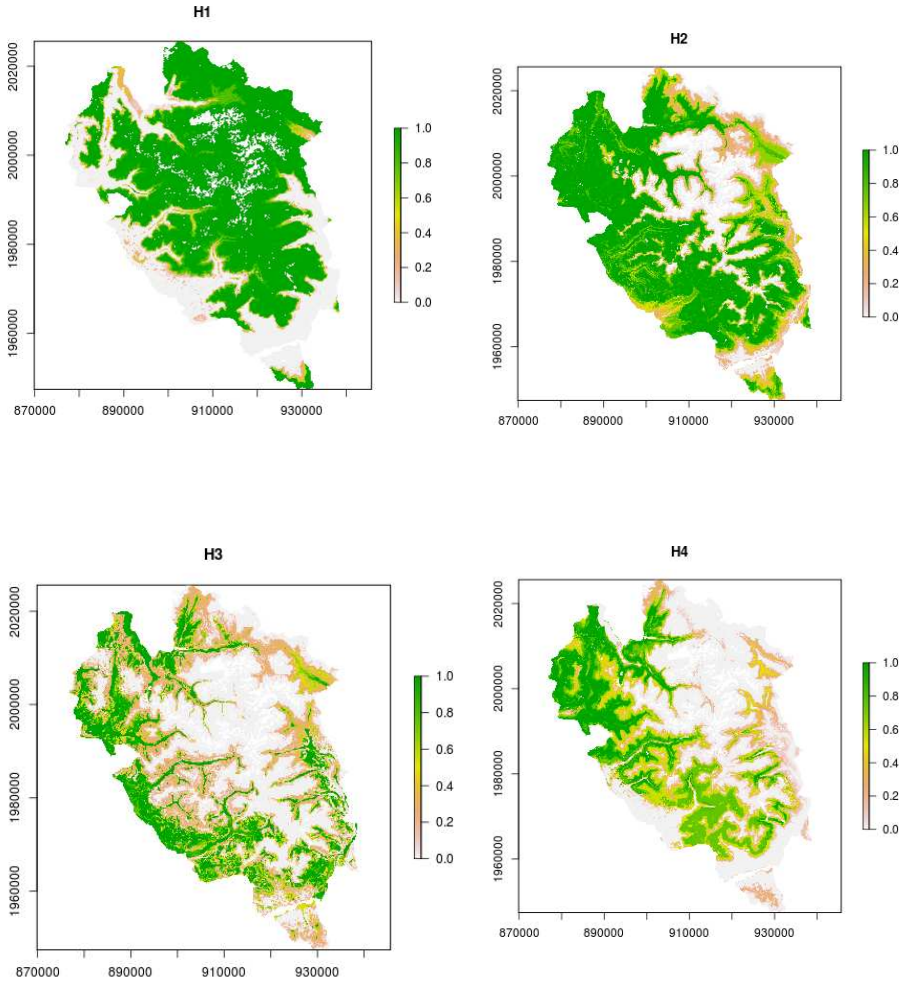
Ensemble Forecasting:

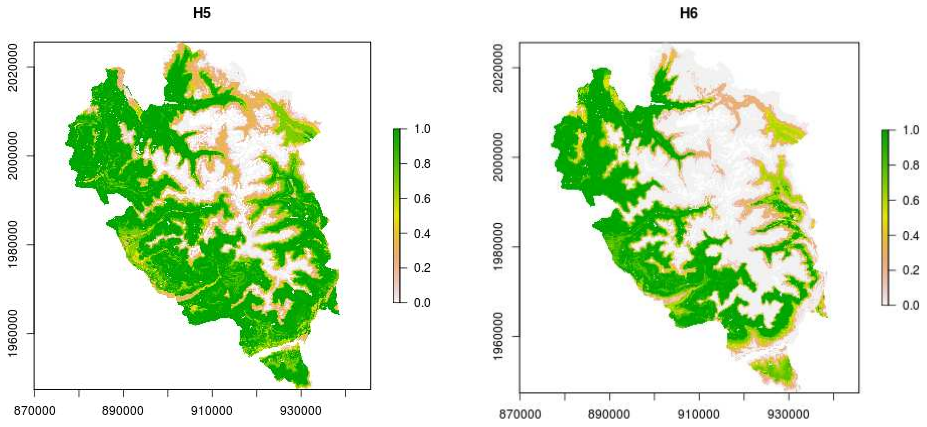
We used an ensemble forecasting to derive consensus probability of our PFG distributions, as follow: 1) We projected of all models 2) We transformed the probabilities of presence into presences and absences according to the thresholds optimized by TSS in the evaluation

procedures 3) We calculated the sum of all binaries projections weighted by their TSS score 4) We rescaled the projection (between 0 and 1) by a division by the maximum TSS.

Fig.IV.S1 : The PFG current habitat suitabilities. This set of 3 figures represents the current habitat suitability for (a) Herbaceous, (b) Phanerophyts and (c) Chamaephyts. The habitat suitability varies from 0 (unsuitable area) to 1 (high suitability).

(a)

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H6
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1980000
1960000
870000
890000
910000
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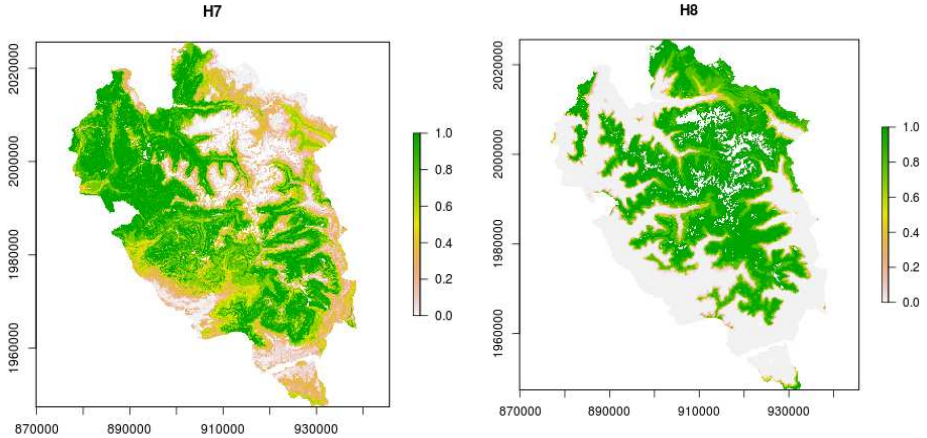
0.4
0.2
0.0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H8
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870000
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930000
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0.8
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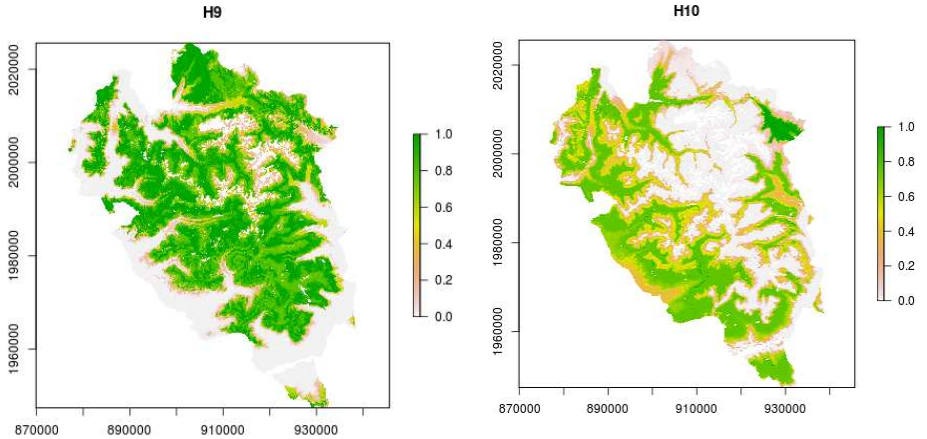
0.4
0.2
0.0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H10
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2000000
1980000
1960000
870000
890000
910000
930000
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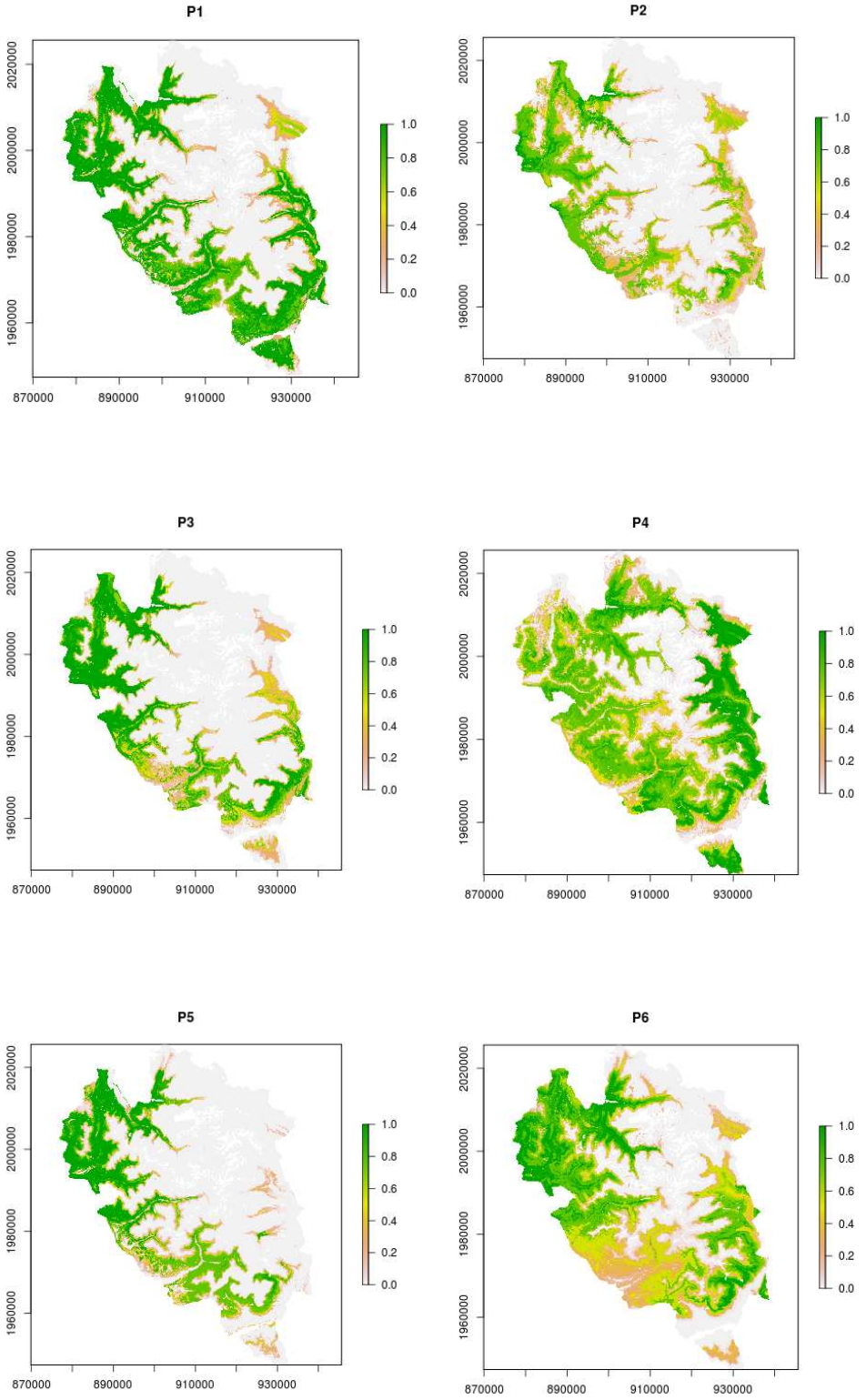
0.6
0.4
0.2
0.0

(b)


P1
P2
P3
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0.6
0.4
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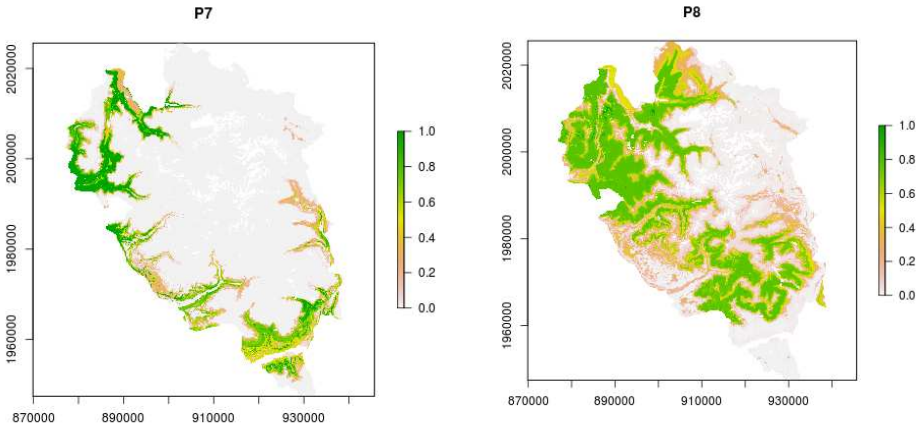
0.0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P8
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0.6
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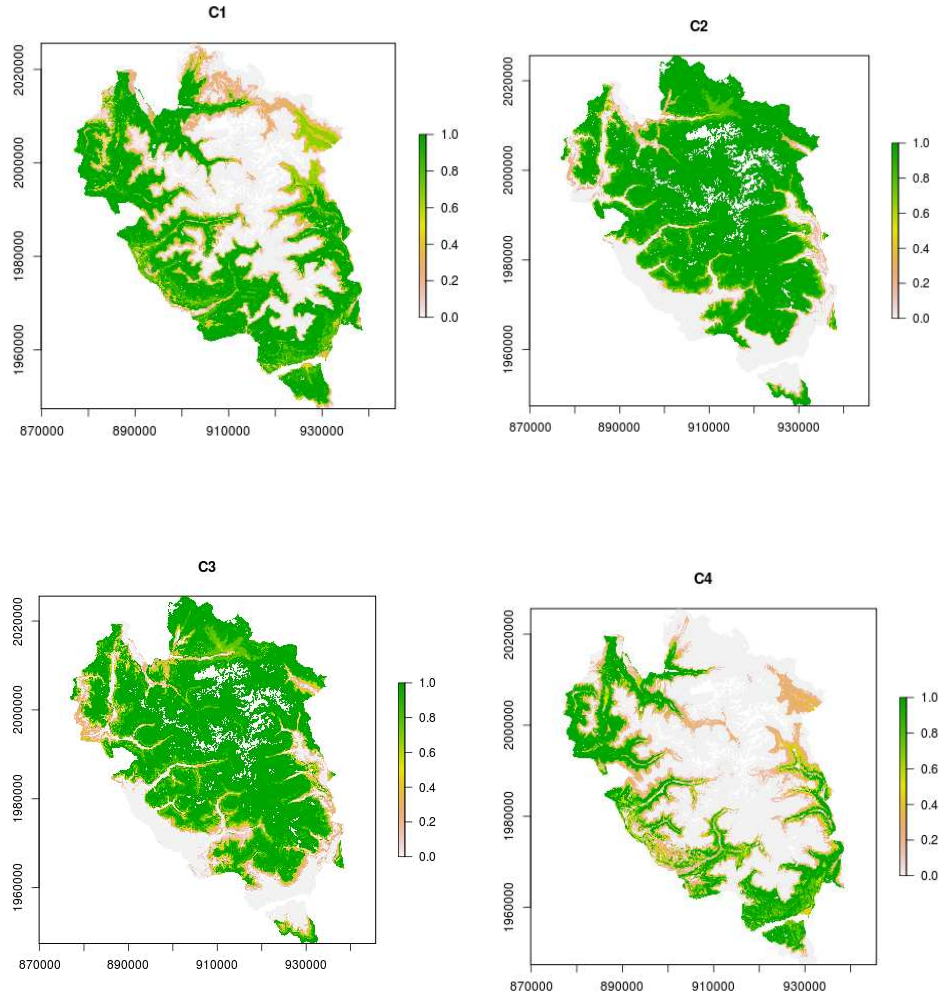
0.0

(c)


C1
C2
C3
C4
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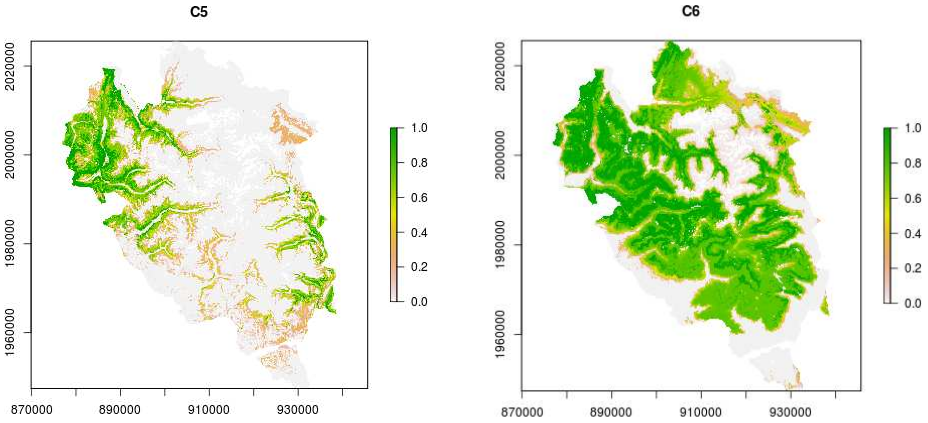
0.4
0.2
0.0


C5
C6
2020000
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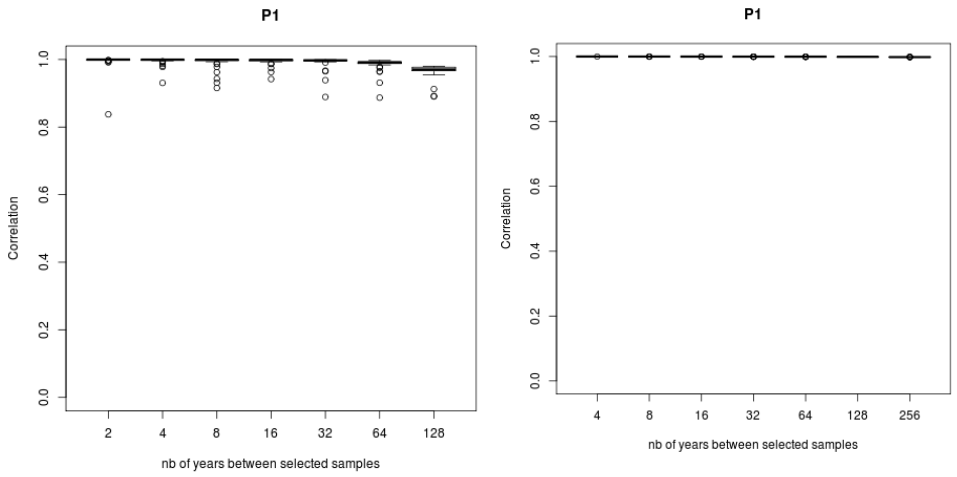
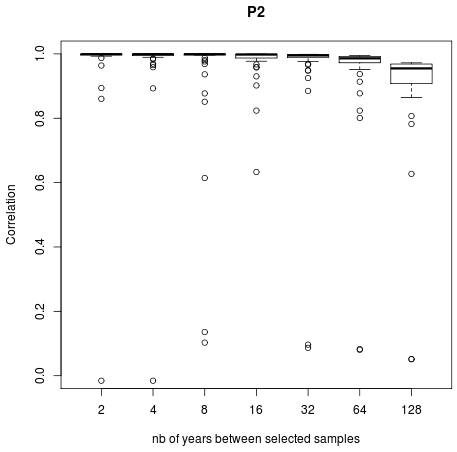
APPENDIX. IV.S4 TEMPORAL AND INTER-REPETITIONS VARIABILITY

We studied the point-to-point correlation between different times of a 600 years simulation. For this simulation we started with an empty landscape, we added seeds (seedling) during the 100 first years (other tests were made to show that it's enough for our study case), then we let the vegetation involve during 500 years.

We showed that during the colonization phase (200 first years), the landscape was changing, but the PFG abundances distributions reached equilibrium after few years (see **Fig.IV.S2** for Phanerophyts dynamic).

Fig.IV.S2 : The PFG point to point total abundance time correlation. The following graphs represent the distribution of the point to point correlation of the PFG abundances, between couple of years separated by 2, 4, 8, 16, 32, 64, 128 or 256 years. It can be interpreted as a temporal variogram. The left column contains temporal correlations made on the 200 first years of a simulation (Seedling and establishment time). The right column contains temporal correlations made on the following 400 years.

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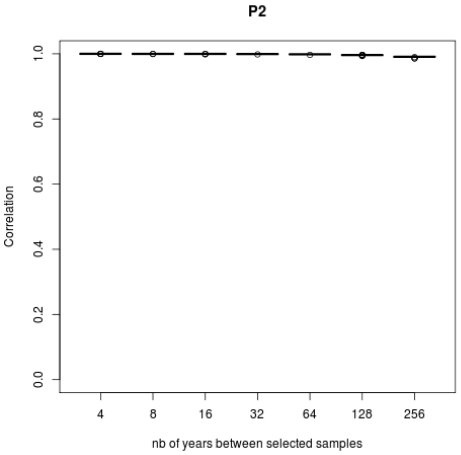
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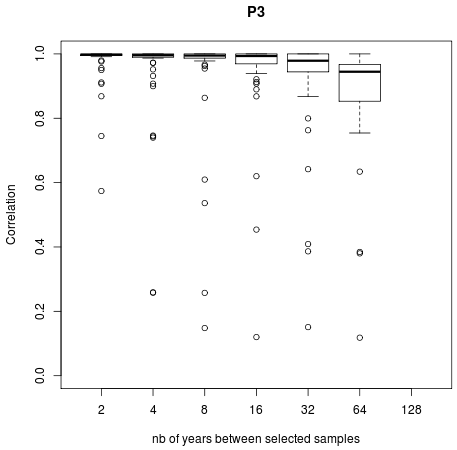
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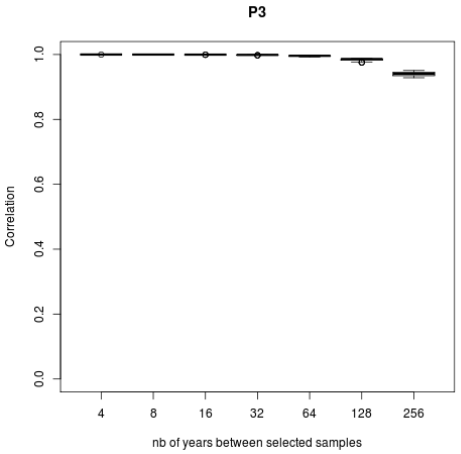
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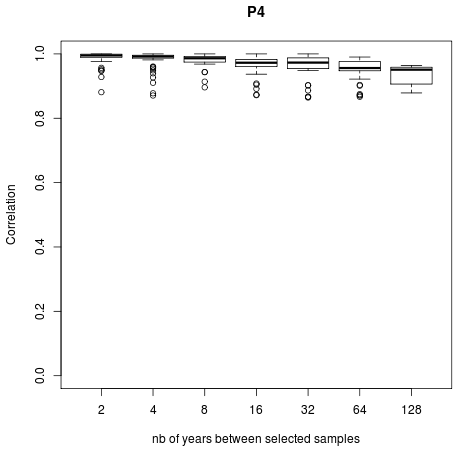
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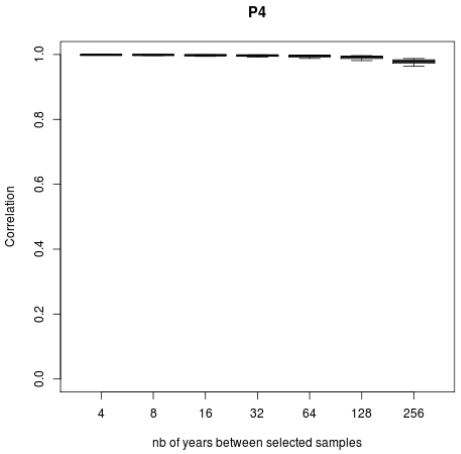
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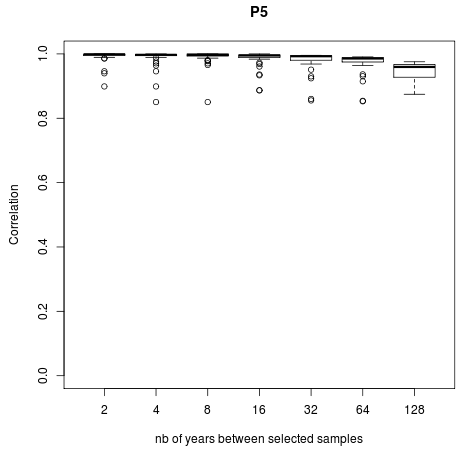
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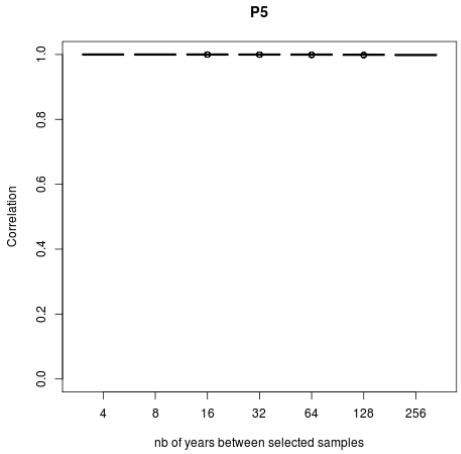
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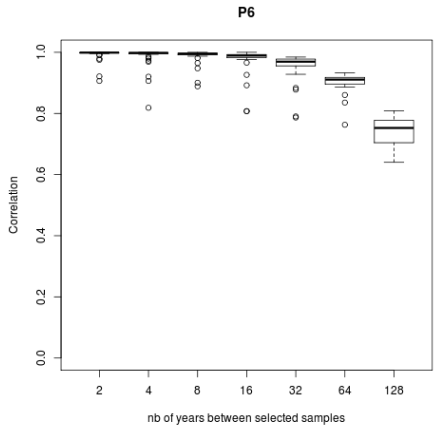
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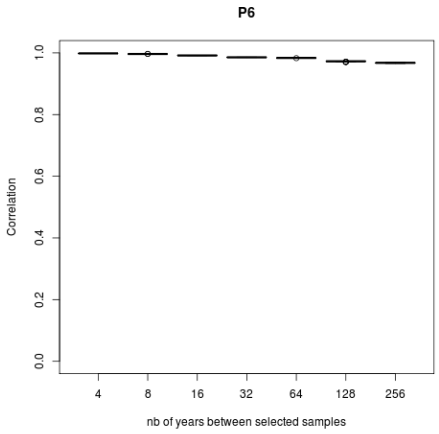
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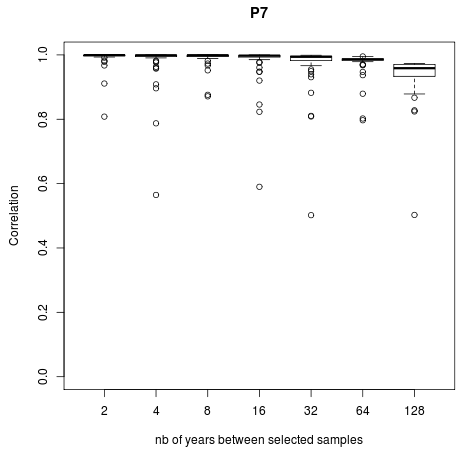
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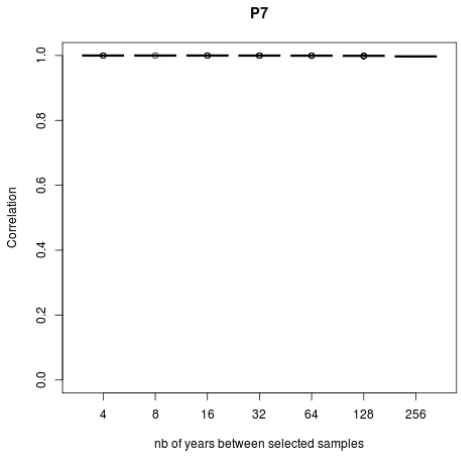
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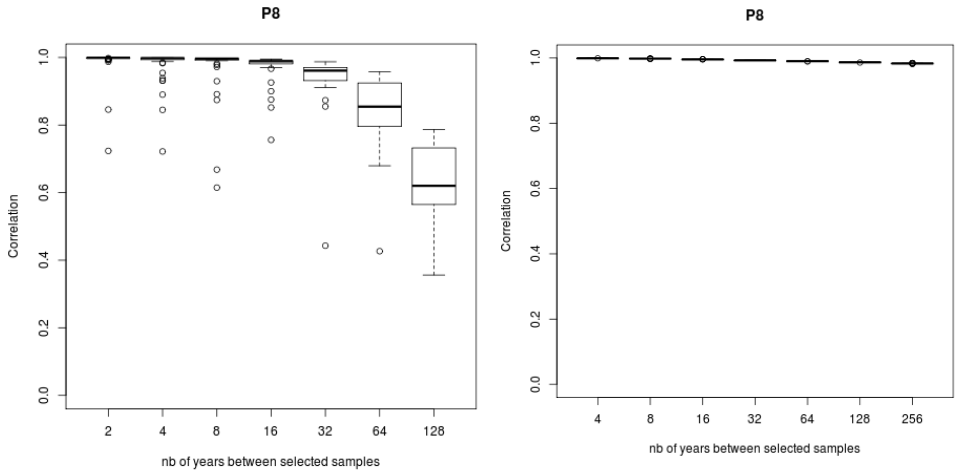


Tab.IV. S1 : Inter-Repetition outputs correlations. This table contains the Pearson's correlations scores between 3 repetitions of the FATE-H simulation presented in the study. We considered the 200 years following after stabilization (100 years of seedling and 100 years of burn-out). We compared the average abundance in each strata across the 200 years.

	Abundance in strata 1 (0-1m)	**Abundance in strata 2 (1-4m)**	**Abundance in strata 3-5 (above 4m)**
Rep1 vs Rep2	0.933	0.999	0.998
Rep1 vs Rep3	0.788	0.979	0.979
Rep2 vs Rep3	0.757	0.977	0.979

CHAPITRE V:

CONSEQUENCES OF CLIMATE AND LAND USE CHANGE ON THE VEGETATION STRUCTURE AND PLANT FUNCTIONAL DIVERSITY IN THE ECRINS NATIONAL PARK

Boulangeat, I., Georges, D., Dentant, C., Bonet, R., Van Es, J., Abdulayak, A., Zimmermann, N.E. and Thuiller, W. Consequences of climate and land use change on the vegetation structure and diversity in the Ecrins National Park. *In preparation.*

Abstract

Modeling tools offer the possibility to quantify the potential impacts of global change on biodiversity. However, very few are adapted to be used at regional scales where management decisions are actually made. The main consequence is that low confidence is given to projections at this scale. New kinds of models are currently developed to overtake these limitations. These models, called 'hybrid-models' take advantage of both mechanistic and statistical approaches, and should be able to produce more robust scenarios at regional scales and over contrasted landscapes.

Here, we make use of a newly developed hybrid model of vegetation dynamics to simulate the potential impacts of both climate change and management practices on the biodiversity of the Ecrins National Park in the French Alps. We simulated the dynamic of 24 plant functional groups, shown to significantly represent the different facets of vegetation diversity. In partnership with the park managers, we developed three extreme management practices over the national park (no change, grazing intensification and grazing break down).

The effects of management practices on the regional vegetation dynamics was simulated alone but also in interaction with regional climate change. Our simulations showed that after abandonment, the colonisation of grasslands by the forest was rapid. On the contrary, under climate change, there was a time lag before we could observe the colonisation of new suitable areas by trees. The effect of grazing intensification was immediate, reducing the total tree cover, but didn't affected the long-term dynamic induced by climate change. We showed that the functional diversity could increase as a consequence of the abandonment of pastures or during the first years of climate change. However, long-term perspectives for functional diversity under climate change were a general decrease whatever the chosen management.

We conclude that the use of a dynamic and temporally explicit model is necessary to disentangle short-term and long-term perspectives of global changes, and to determine tipping points after which the subtle alteration of the environment may lead to drastic transformations. Our modelling approach with FATE-H also pointed out the interest of accounting for spatial and temporal mechanisms in models, in order to understand and predict the interplay effects of land-use and climate change in time and space.

INTRODUCTION

The construction of scenarios to predict the future dynamic of the vegetation diversity is a major challenge in ecology (Pereira *et al.* 2010; Bellard *et al.* 2012). To address it, ecological modeling is a privileged tool as it allows the quantification of diversity changes, and the exploration of large time scales. However, most of existing models are unable to give robust predictions at the regional scale (Parmesan *et al.* 2011), where reserve networks (e.g. NATURA 2000) and protected areas are designed and most of conservation decisions are made.

To overcome the limitations of existing models, new approaches have been recently developed (Gallien *et al.*, Boulangeat *et al.* Chapter IV). They are usually based on a combination of mechanistic and phenomenological models (Wintle *et al.* 2005; Keith *et al.* 2008; Anderson *et al.* 2009). The inclusion of mechanisms allows to account for the processes driving species distributions and co-existence and should improve the robustness of predictions, and the use of statistical models permits to decrease the calculation time and allow increasing the extent of the study or the number of modeling entities (Chapter IV). These models are thus particularly adapted to investigate the potential impacts of environmental change scenarios at regional spatial scales and over realistic time-scales.

Amongst the five major drivers of changes on biodiversity (climate, land use change, nitrogen deposition, atmospheric CO2, biotic exchange, Sala *et al.* 2000, Thuiller 2007), climate and land use are expected to be the most prominent in temperate countries in the near future. Climate, which has been recognized as a first order factor to determine species diversity (O'Brien *et al.* 2000; Whittaker *et al.* 2001), is expected to drastically change in the next century (IPCC 2007b). As a consequence, every component of biodiversity might be affected through various means (e.g. change in phenology, distribution and physiology, Bellard *et al.* 2012). The on-going climate change has already been shown to impact species distribution and biodiversity (Parmesan 2006; Lenoir *et al.* 2010; Gottfried *et al.* 2012) and more particularly causing a shift of the tree line

at highest elevations (Randin *et al.* 2009a). Although climate is a key driver, changes in land-use and practices is also known to strongly influence the vegetation structure and diversity (Foley *et al.* 2005). This is particularly true in rural landscape and mountain systems where past land uses over centuries have shaped the current landscape (Quetier *et al.* 2007; Quetier *et al.* 2010). In Europe, two main trends of land use changes have been observed in the past decades. On one hand, the agricultural crisis has led to a drift from the land, resulting in shrub and tree encroachments in old pastures and cultivated lands (Gehrig-Fasel *et al.* 2007). On the other hand, lowland areas have seen a dramatic increase in intensive agriculture and farming leading to unprecedented rates of local species extinctions (Hodgson *et al.* 2005). There is thus a crucial need to investigate the interplay between climate and land use changes and its impacts on biodiversity at regional scales.

Here, we use a hybrid dynamic vegetation model called FATE-H, which is able to model the vegetation dynamics with enough details to represent the vegetation structure and the plant functional diversity at the regional scale (chapitre IV). We analyzed the short and long term consequences of land-use and climate changes, taken separately and their interplay, on the regional biodiversity of the Ecrins National Park (PNE). The PNE is a national park located in the French Alps, relatively large for Europe. It harbors a heterogeneous landscape due to a complex topography and a large proportion of its surface is being moderately to intensively grazed by domestic stock.

For this particular exercise, and in partnership with the PNE managers, we developed three land use change scenarios: no changes, domestic grazing intensification, and domestic grazing abandonment. Our expectations was that the effects of climate change should likely be visible at the sub-alpine belt, where species were expected to shift their distributions upward (Jump *et al.* 2012), and the forest to colonize higher elevations (Randin *et al.* 2009a). The abandonment of domestic grazing should have a similar effect that is the colonization of abandoned pastures by the forest. An intensification of grazing should reversely maintain open environment and compensate the effect of climate. Finally,

species diversity was expected to decrease, at short term, in both land-use abandonment and land-use intensification scenarios (Niedrist *et al.* 2009).

MATERIAL AND METHODS

(a)The dynamic hybrid model

We simulated the vegetation dynamic with a spatially and temporally explicit model called FATE-H (see chapter IV). This hybrid-DVM combines the strengths of different sub-models and simulates the spatial and temporal dynamics of plant functional groups (PFGs) in an annual time-step. The region of interest was represented as a grid of 100x100m resolution. A succession model, simulating the demography (e.g. fecundity, recruitment and mortality) of PFGs and the competition for light between the PFGs, was run within each grid cell (adapted from Moore & Noble 1990). The total recruitment of each PFG within each grid cell was influenced by topo-climatic suitability of the pixel estimated using a habitat suitability model (Guisan & Thuiller 2005). The spatially explicit processes between grid cells was simulated through a seed dispersal model, in which the proportion of dispersed seeds was determined by the abundance of mature PFGs. Seed dispersal distance was function of the PFG dispersal parameters and a stochastic function (see Chapitre IV). The recruitment and then survival of the seeds within each pixel depended on the light availability in the pixel and the PFGs light preferences. A disturbance model was also included to simulate the effects of both grazing and mowing. These two disturbances influenced the abundance of juveniles and mature plants differentially depending on the sensitivity and response of each PFG to the intensity and frequency of the two disturbances (see chapter IV for details). In this study, we used three intensity levels for grazing.

We modelled 24 PFGs, determined by an emergent group approach (Lavorel *et al.* 1997; Herault 2007) in which the dominant species of the area were grouped based on a selection of six key species characteristics and using a classification procedure (see chapter III). Species were first

classified based on their biological types to make a coarse selection on demography (long-lived versus shirt-lived). Then, for each biological type, we grouped species with similar topo-bioclimatic niches (species with similar niches are expected to be influenced in the same way), similar plant height and light preferences (to group species with similar behaviour face to the competition for light), similar dispersal distance class and similar palatability (see chapter III for details). The classification procedure (i.e. UPGMA) aimed at maximising intra-group homogeneity and maximising inter-group impurity.

(b)Climate and land use change scenarios

The potential effect of climate change was modelled by habitat suitability. For each PFG, current and future topo-climatic suitabilities were projected over the gridded region of interest. As stated above, the habitat suitability influenced then seed recruitment. We used BIOMOD to calibrate a range of statistical models over the 24 PFGs and used an ensemble forecasting to summarise the uncertainty coming from those techniques (Thuiller *et al.* 2009). For future climate, we decided to focus on the A1B scenario, as the variation between scenarios at our resolution and spatial scale were rather minor. Future climate was simulated by the regional climate model "ssmhi_rca30_ccsm_ar4" that we downscaled at 100x100m resolution. Climate change was simulated for the next 100 years, with a gradual change every 15 years. For the following years, we kept the climate constant as projected in 2100.

Three options of land-use management were considered, in interaction or not with climate change. First, as a baseline, we kept the grazing and mowing conditions constant in the future. The second scenario simulated a situation where all grazing activities would be abandoned in the coming five years. We hypothesized this situation as a breakdown of European support to agriculture. At the opposite, a third scenario reflected an extreme case where all potential pastures would be intensively used in the coming years. According to the PNE managers, this scenario was likely to happen if repeated drought would occur in southern France and would ultimately increase the demand for the use of the PNE' pastures in

the summer season. We made here the hypotheses that our local land-use change scenarios were not constrained by global socio-economic scenarios.

(c)Biodiversity measures

We analyzed the dynamics of two different aspects of the vegetation. First, in order to compare our results with previous work, the evolution of canopy closure in each elevation belt was examined for all scenarios. It was measured by the percentage of vegetation above one meter, which has been shown to well-differentiate between open and closed habitats (chapter IV). In a second analysis, we looked at the evolution of alpha and beta diversity ("true beta diversity", Jost 2007; Tuomisto 2010), in each altitudinal belt. We computed the 'true' alpha diversity in each pixel using the 24 modeled PFGs and their relative abundances. As a consequence, this is a measure of functional diversity rather than species diversity. Beta diversity was calculated in each vegetation belt.

(d)Simulations

The initial state was determined by a first simulation, where the first 100 years consisted in a seedling (seeds of all PFGs were added in all cells every five years). This time was necessary for forests to set up where the environment was favourable for them. The following 300 years composed the burnout, and the initial state was defined right after. Given that the dynamic of the vegetation was little affected by the internal stochasticity of the model (see Supplementary Material in chapter IV), we present only one repetition for each scenario for the sake of simplicity. In an independent simulation, colonization speed was tested and we concluded that it was appropriate to interpret vegetation change on the time scale considered (from now to the next 450 years). After this initial state, climate changed every 15 years during 90 years and stayed the same in the following 400 years. Land-use changes were applied during the 10^{th} year.

RESULTS

The effect of land use intensification was a reduction of closed environments. Surprisingly, the simulated response of the vegetation was pretty fast in this case (Fig. V.1a). On the contrary, grazing abandonment led to an increase of canopy closure except at the highest elevations (Fig.V.1a). However, in this situation, the vegetation needed about 250 years to reach a new equilibrium.

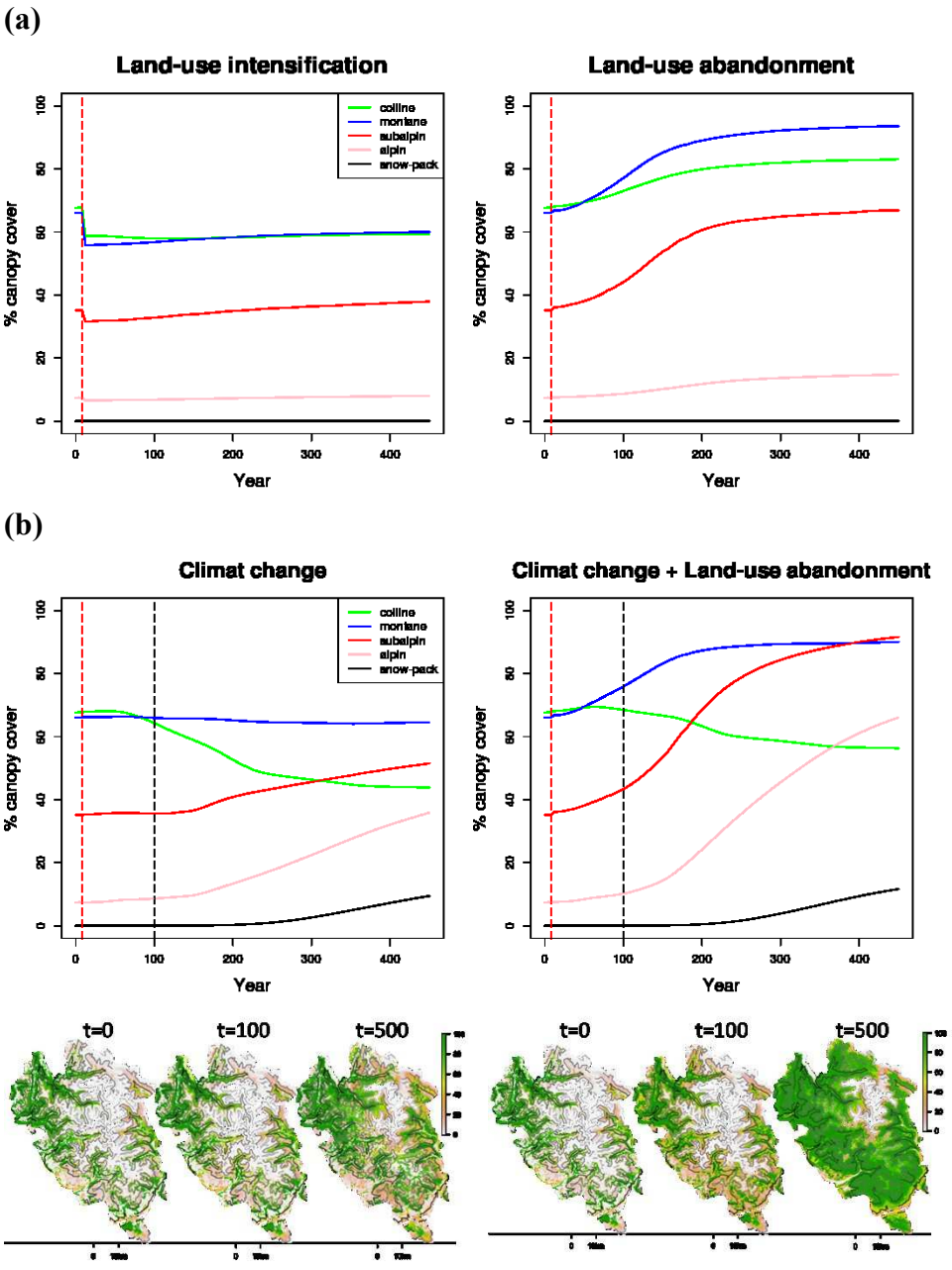


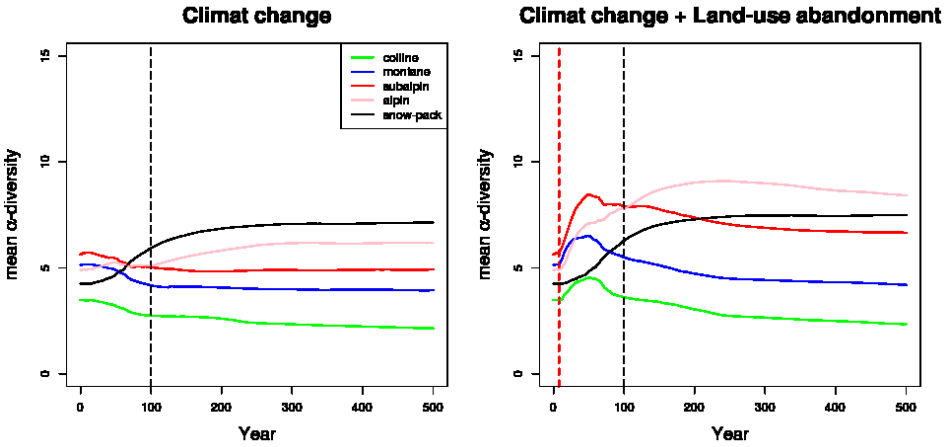
Fig. V.1 Evolution of the canopy closure in five altitudinal strata, for four scenarios. Colline (800-900m); montane (900-1600m); subalpin (1600-2250m);alpin(2250-2950m);snow-pack (2950-4100m) The red vertical line indicate the time when the land-use change scenario are applied. The black vertical line indicates the end of climate change **(a)** Evolution of the canopy cover in two land-use scenario. Intensification and abandonment are simulated age year 10. **(b)** Evolution of the canopy covers under climate change scenarios, alone and in combination with land-use abandonment. The percentage of cover is mapped for three key years (0, 100, 500) below the x-axis.

Under climate change only, we also found the expected trends. However, during the simulated time of climate change (0-100 years), there was

very little variation in vegetation cover (Fig.V.1b). The effects were only visible after 100 years showing a certain time-lag in the overall response. Therefore, vegetation was barely stabilized 400 years after climate change stopped. The tree cover increased in higher elevations (subalpine, alpine and snow-pack), showing a colonization dynamic. In the montane belt, the tree cover kept equal, suggesting a potential replacement of the forest tree identity (Fig.V.1b). The forest cover decreased in the lowest part of the altitudinal gradient. However, this last result must be interpreted with precaution as these areas were situated at the edges of the PNE, which might be subject to edge effects and colonisation from low-lands areas not modelled here. The combined effects of land-use abandonment and climate change led to a rapid colonization of the pastures at the lowest elevation first, and then at higher elevations (Fig. V.1b). Long term effects concerned mainly the subalpine colonization by trees, leading to a landscape dominated by the forest at year 500. The intensification of land-use did not change the dynamic of vegetation response to climate change, both effects being separated in time (results not shown here, see Fig. V.S2).

Climate and land-use changes affected both alpha and beta diversity components. Under climate change, contrary to the response of the vegetation structure, the mean alpha diversity changed during the first 100 years with an overall decrease except at high elevation, were new spaces were probably colonized (Fig. V.2a). The beta diversity was simulated to generally increase under climate change only, but later, when alpha diversity stabilized (Fig. V.2b). In a scenario where climate change and land abandonment interplayed, both diversity indices evolved differently. They generally increased during the climate change phase (the first 100 years) and then decreased to recover their initial value or even a lower value (Fig. V.2), except at higher elevations. Interestingly, the breakdown of land abandonment in the first five years increased the beta diversity abruptly, but decreased afterwards during the climate change phase. The combination of land-use intensification and climate change showed no interacting effects on diversity measures (Fig. V.S2).

(a)



(b)

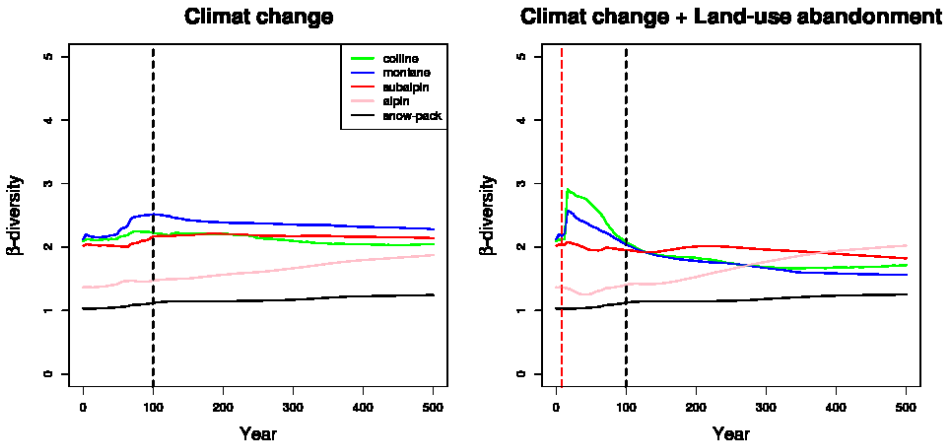


Fig. V.2 Evolution of the diversity in five altitudinal strata, for two scenarios. Climate change alone and in combination with land-use abandonment. Colline (800-900m); montane (900-1600m); subalpin (1600-2250m);alpin(2250-2950m);snow-pack (2950-4100m) The red vertical line indicate the time when the land-use change scenario are applied. The black vertical line indicates the end of climate change **(a)** Evolution of the average alpha diversity. **(b)** Evolution of the true beta diversity.

DISCUSSION

The dynamic of the vegetation simulated with our newly developed spatially and temporally explicit model of vegetation (Fate-H) under both climate change or land use abandonment gave interesting trends that were in general consistent with previous studies and forecasts (Dullinger *et al.* 2012). However, we showed that the time to reach equilibrium might greatly differ between scenarios. After abandonment of grazing and mowing, the forest would colonize herbaceous ecosystems relatively rapidly (Fig. V.1a). This phenomenon has already been observed during the last decades (Gehrig-Fasel *et al.* 2007). The vegetation dynamic under climate change was similar but took much more time, suggesting an important time lag usually not considered by modelling studies using simple statistical habitat modelling (Fig. V.1b).

The combination of land-use intensification and climate change showed neither interacting effects on tree cover dynamic (Fig. V.S2), nor on the diversity response (Fig.V.S3). This result could be explained by the immediate response of the vegetation to intensification of grazing and mowing, resulting in a reduced tree cover (Fig. V. S2) and diversity (Fig. V.S2). This response did not seem to interact with the response to climate change, having longer term impacts. On the contrary, the combination of climate change and land-use abandonment showed very strong interacting effects. In this situation, the colonization of herbaceous ecosystems by trees was not limited. Following abandonment of grazing and mowing, climatic suitable areas were colonized immediately (Fig.V.1), and trees occupied a larger part of their suitable habitat (intermediate elevations, Fig.V.1b). In a second time, when the climate became suitable at higher elevations, the colonization of these areas was relatively fast compared to a climate change scenario alone. This result might be explained by a dispersal effect. Indeed, if trees had already colonized neighbouring habitats, the dispersal distance to new ecosystems decreased, and consequently, the colonization of sub-alpine and alpine belts was immediate. The interactions also affected the evolution of diversity patterns (Fig. V.2). In the absence of climate

change, alpha and beta diversity increased as a result of land-use abandonment, and then stabilized. Climate change modified this dynamic in a long-term perspective, which resulted in a final decrease for both alpha and beta diversity.

Conclusion

Our simulations highlighted the importance of the time required for ecosystems to respond to environmental changes. We showed that, even if no or little effect is detected during the continuous change in climate, strong modification in the vegetation dynamics response might be then seen over 400 years. Short and long term effects are thus inter-wined and difficult to tease-apart when all potential changes are put together. Our simulations based on climate only, land use change only, and then interactions between the two drivers allowed to disentangle their respective effects and demonstrated the difficulty to make realistic projections within a simplified modelling exercise. Concerning diversity changes, we showed that the functional diversity could increase as a consequence of environmental changes, whereas previous studies, focusing on species diversity, generally predicted a decline in species richness (Niedrist *et al.* 2009).

SUPPORTING INFORMATION

Dynamic colonization time

To check the colonization dynamics of vegetation in FATE-H, we selected three areas in the Ecrins National Park, and averaged the results. Grazing was maintained during 100 years and then stopped. We aimed at estimating the time required by the forest to colonize the abandoned areas. We showed that the forest was able to settle in the following 40 to 140 years. The difference between elevations (with varying habitat suitability for trees) was the final proportion of canopy but the colonization dynamic was similar. All these observations seem to be plausible compared to observations in the region, due to recent land-use abandonment.

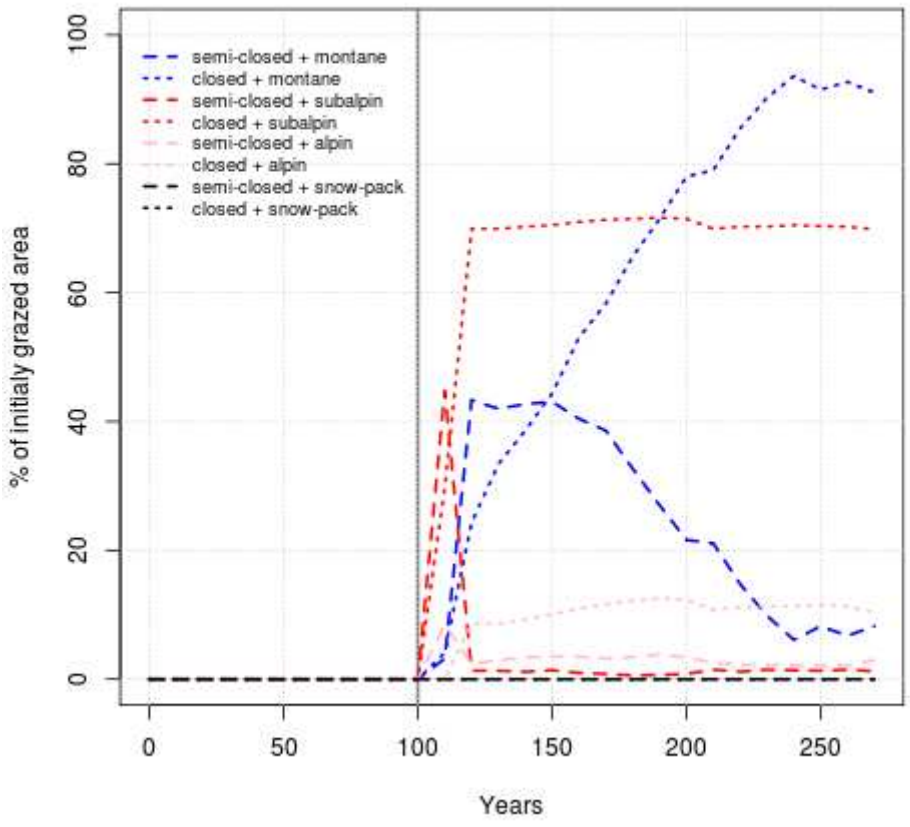


Fig.V.S1: Evolution of the proportion of semi-closed and closed vegetation areas in the former grazed pixels. We determined the canopy closure by the percentage of vegetation above 1 meter. Semi-closed areas correspond to 40-60% of canopy cover. Closed areas were defined by a canopy cover higher than 60%. The different lines show the colonisation dynamic in three selected areas. Blue: in the montane vegetation belt (900-1600m). Red: in the subalpin vegetation belt (1600-2250). Pink: in the alpin vegetation belt (2250-2950m). The black lines corresponded to snow-pack pixels (higher than 2950m).

Fig. V.S2 Evolution of canopy covers under climate change and land-use intensification:

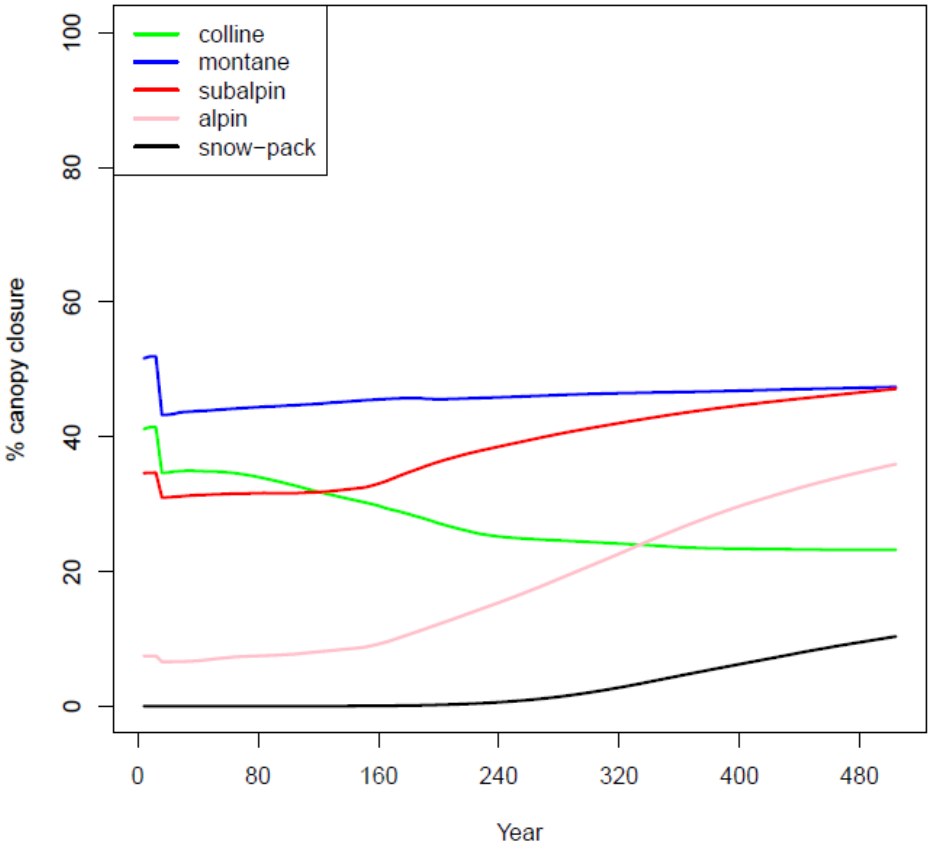
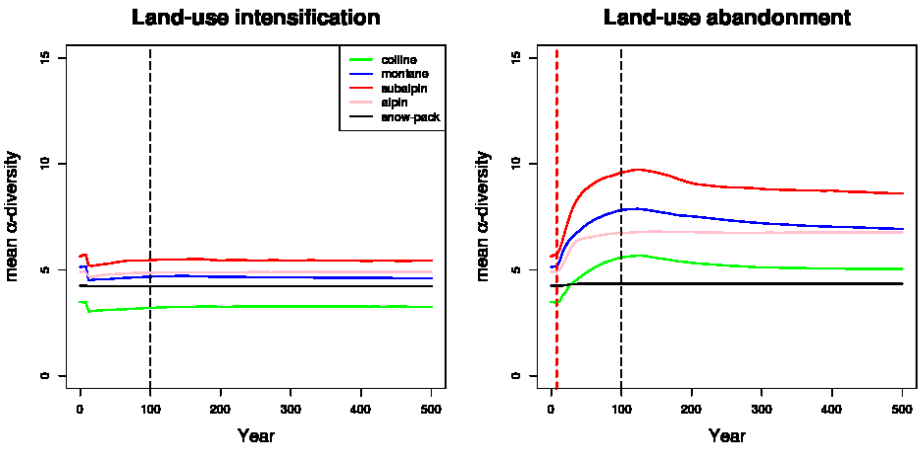
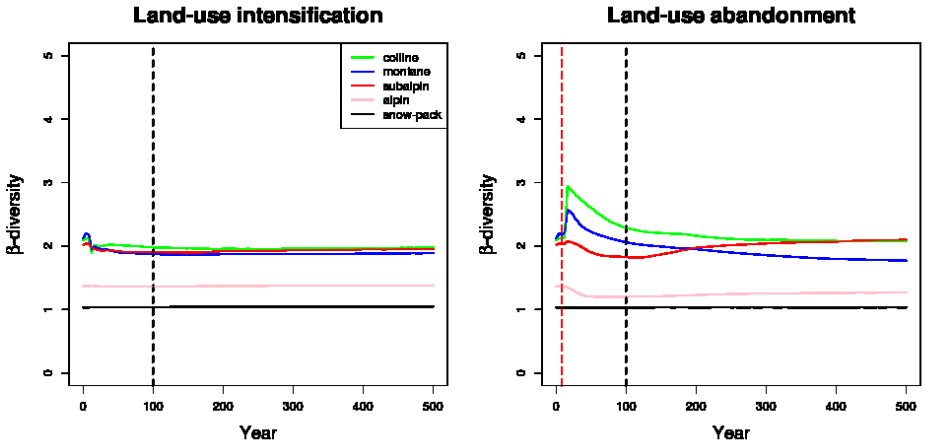


Fig. V.S3 Evolution of diversity indices under land-use scenario. (a) alpha diversity (b) beta diversity

(a)



(b)



SYNTHESE : DISCUSSION GÉNÉRALE ET PERSPECTIVES

COMPRENDRE LES MÉCANISMES DE COEXISTENCE

UNE VISION HIÉRARCHIQUE DES MÉCANISMES VALIDEE

Le chapitre II nous a permis de tester l'ensemble du cadre théorique hiérarchique proposé dans l'introduction (Fig. i.7). Nous avons trouvé que l'absence (ou la présence) des espèces modélisées était bien décrite par les variables abiotiques et l'indice de dispersion (Fig. II.4a), suggérant l'importance première des mécanismes de filtres environnementaux et de limitation par la dispersion. L'influence secondaire des indices d'interactions biotiques à cette étape pourrait être le résultat de mécanismes d'exclusion compétitive.

L'approche de modélisation emboitée nous a permis de démontrer la nécessité de prendre en compte les mécanismes agissants aux échelles spatiales supérieures pour analyser ce qui se passe au niveau de la communauté. En effet, l'efficacité d'un modèle hiérarchique est largement supérieure à celle d'un modèle traditionnel (Fig. II.S5). Cette méthode nous a permis d'analyser la variation d'abondance des espèces au sein de leur niche, et d'étudier le résultat des mécanismes de coexistence. Notamment, les modèles mettent en évidence l'importance des interactions biotiques négatives, qui peuvent être le résultat de la compétition. D'un autre côté, les facteurs abiotiques ne sont pas négligeables pour expliquer la variation d'abondance d'une espèce. Ils sont même prépondérants pour certaines espèces (Fig. II.4b), ce qui est en accord avec des études où le climat a été relié à la performance des espèces (ex. Riba *et al.* 2002; Thuiller *et al.* 2010b).

LES INTERACTIONS BIOTIQUES

Compétition ou conditions abiotiques locales ?

Nous avons montré dans le chapitre II l'importance des processus qui ont lieu à l'échelle de la communauté pour expliquer l'abondance des espèces, et dans une moindre mesure leur probabilité de présence en un site donné. Cependant, même si l'on suppose que la compétition est un mécanisme important, son effet est très difficile à distinguer des effets

de l'environnement abiotique local qui n'est pas représenté par les variables choisies. À l'intérieur de la communauté, les conditions abiotiques peuvent également être modifiées par la présence d'autres espèces (ex. la canopée modifie la température près du sol). Le seul moyen d'être certain de la présence d'une certaine forme de compétition est de la tester expérimentalement, ce qui est impossible lorsqu'on étudie toute une flore à l'aide de données empiriques.

Spécialisation et stratégie compétitive

La différenciation de niche permettrait à deux espèces de coexister parce que leur compétitivité se croise le long d'un gradient, chaque espèce dominant l'autre dans certaines conditions (Fig. i.3 ; Chesson 2000a ; Silvertown 2004). Nous avons étudié les patrons de spécialisation (de largeur de niche) dans le chapitre I et deux principales hypothèses peuvent être formulées pour expliquer la restriction de l'amplitude écologique des espèces. Les résultats nous ont montré que les espèces compétitrices sensu Grime (Fig. I.5) sont plutôt généralistes (de largeur de niche étendue) alors que les espèces spécialistes (de largeur de niche restreinte) sont plutôt tolérantes au stress (Fig. I.5b). Ces tendances nous suggèrent que dans de nombreux cas, la spécialisation est le résultat de l'exclusion d'espèces par de meilleures compétitrices, dans les milieux les plus productifs. Les perdantes se réfugient alors dans des milieux plus stressants (Bonesi & Macdonald 2004), où la compétitivité de leurs concurrentes est réduite et où elles seront alors dominantes. Par conséquent, ces spécialistes se différencient à la fois par une largeur de niche restreinte et par une marginalité sur un gradient de productivité (ou stress) non déterminé. D'un autre côté, certaines spécialistes sont plutôt compétitrices (Fig. I.5b), et donc le premier scenario ne peut pas s'appliquer à celles-ci. Dans ce cas, la faible amplitude écologique peut s'expliquer par une faible tolérance aux milieux peu productifs. En contrepartie, ces spécialistes auraient une compétitivité augmentée dans les milieux fertiles (Wisheu 1998). Ces deux situations suggèrent qu'un des axes importants de différenciation de niche est celui de productivité. Cependant, l'amplitude écologique mesurée dans le chapitre I mélange

tous les gradients et ne caractérise pas la position de niche grâce à des données environnementales. L'approche de mesure de la spécialisation par analyse des patrons de cooccurrence d'espèces permet de capter tous les axes de spécialisation, même ceux liés à des conditions micro-environnementales, généralement difficiles à caractériser avec les données disponibles (ex. type de sol), mais ne permet pas de distinguer les différents types de spécialisation.

Vers une séparation des gradients de différenciation

Afin de mieux comprendre les mécanismes de différenciation de niche, il serait très intéressant de séparer la spécialisation Grinnellienne et la spécialisation Eltonienne chez les plantes (Devictor et al. 2010). En ce qui concerne la niche Eltonienne chez les plantes, la manière de la mesurer et de l'interpréter n'est pas évidente. La position pourrait être définie par le rôle fonctionnel d'une espèce et une spécialiste aurait un rôle marginal (ex. une fixatrice d'azote). La largeur de niche pourrait être définie par la variabilité de ce rôle à travers les individus, les populations, ou au cours du temps. Une approche pourrait être l'utilisation de traits fonctionnels et leur variabilité intra-spécifique. D'un autre côté, la spécialisation écologique totale mesurée par le biais des cooccurrences résulte à la fois de la spécialisation grinnellienne et de la spécialisation eltonienne. Une approche indirecte serait d'utiliser les résidus d'un modèle « spécialisation totale ~ spécialisation Grinnellienne », qui décrirait la diversité des interactions biotiques possibles.

Nous avons exploré cette piste lors dans le cadre de ma thèse, en utilisant la même approche que celle du chapitre I (Fridley *et al.* 2007), appliquée à une mesure de diversité fonctionnelle. La niche eltonienne a ainsi été caractérisée par le « turnover » fonctionnel des communautés dans lesquelles l'espèce se trouvait. La spécialisation totale a ainsi pu être décomposée en deux axes indépendants. La spécialisation grinnellienne, mesurée par une méthode d'analyses multivariées (Outlying Mean Index, Dolédec *et al.* 2000) et impliquant des variables topo-climatiques importantes, était relativement indépendante de la

spécialisation eltonienne ainsi estimée, toute deux contribuant à la spécialisation totale. Autrement dit, le « turnover » fonctionnel des communautés ou une espèce est présente semble peu lié au « turnover » bioclimatique. Cependant, le « turnover fonctionnel » ainsi mesuré peut représenter d'autres différenciations de niche qui sont locales, et qui n'ont rien avoir avec les interactions biotiques. Finalement, cette décomposition nous a montré que la différenciation de niche peut être décomposée sur un axe de gradients régionaux (mesuré par les gradients topo-climatiques ici) et sur un axe de gradients locaux (mesuré par le « turnover » fonctionnel des communautés). Cependant, la niche eltonienne n'a pas pu être vraiment caractérisée.

Le principal problème à résoudre pour appliquer une telle approche chez les plantes est peut-être de mieux définir la niche eltonienne des espèces végétales. En effet, ce concept est à l'origine basé sur les relations trophiques (Elton 1927) et n'est pas évident à appliquer pour les plantes. Si la niche Eltonienne représente l'environnement biotique, est-il possible de la mesurer par la structure fonctionnelle de la communauté ? Et quelle mesure choisir dans le cas échéant ? Un trait moyen ? Une divergence fonctionnelle ? En conclusion, nous pensons que la décomposition des spécialisations grinnellienne et eltonienne seraient plus facilement applicable chez les animaux, comme les oiseaux par exemple, où la niche eltonienne est bien caractérisée par des types de ressources et d'acquisition des ressources.

Quel type de compétition entre en jeu ?

Une perspective intéressante serait de mettre en évidence le lien entre la compétition et la spécialisation sur un gradient bien identifié. Ceci a été exploré mais non présenté précédemment. Nous avons ainsi tenté d'expliquer la tolérance bioclimatique des espèces, par un ensemble de traits qui décrivent les stratégies d'acquisition des ressources (Grime *et al.* 1997; Reich *et al.* 1999). Dans ce travail annexe, l'analyse des pistes (qui analyse la structure causale entre variables à l'aide de corrélations partielles) nous a suggéré que, dans notre zone d'étude, la capacité de compétition pour la lumière plutôt que la stratégie d'utilisation des

ressources (acquisition-conservation) augmenterait la tolérance bioclimatique des espèces végétales (Fig. s.1). Dans un travail sur les plantes endémiques ayant des aires de distribution restreintes (donc ayant une amplitude climatique particulièrement réduite), Lavergne *et al.* (2004) n'avaient pas non plus identifié de relation entre les traits relatifs à l'acquisition ou la conservation des ressources et l'endémisme. Seule la hauteur, qui peut être interprétée comme un indicateur de compétitivité pour la lumière, était significativement liée à l'endémisme. Ces analyses soulignent que la capacité de compétition pour la lumière est un facteur prédominant de l'amplitude géographique ou climatique des espèces, et a certainement joué un rôle dans la différenciation des espèces le long des gradients environnementaux.

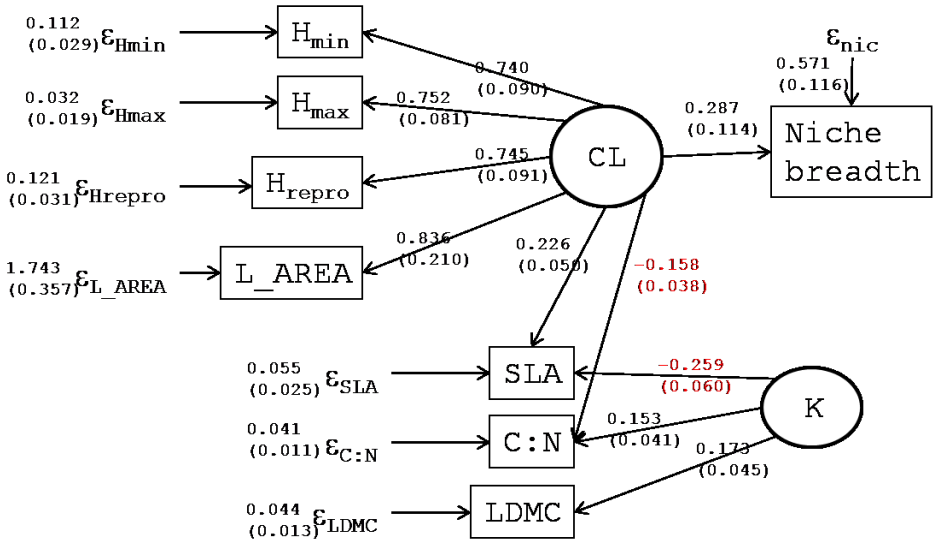


Fig. s.1. Structure causale de l'analyse des pistes. Sont notés les coefficients de piste, les variances résiduelles et leurs erreurs standardes entre parenthèses. La variable latente CL représente la compétition pour la lumière et la variable latente K la stratégie conservatrice. H_{min}, H_{max} et H_{repro} désignent les hauteurs de végétation et de reproduction. Quatre traits foliaires ont été utilisés. La surface des feuilles (L_AREA), la surface par unité de masse (SLA), la teneur en matière sèche (LDMC) et le rapport des teneurs en carbone et azote (C :N). La largeur de niche a été déterminée par une approche multivariée (OMI, « outlying mean index »), impliquant 10 variables topo-climatiques (variables de température, pente, altitude, indices topographiques, humidité de l'air et variables de radiation). L'analyse a été effectuée dans les communautés d'herbacées uniquement.

Démêler coexistence et cooccurrence

Il est important de noter que les données de communauté dont on dispose ne permettent pas de distinguer la cooccurrence de la coexistence. En effet, on suppose que l'image de la communauté prise un jour d'une année est représentative de la structure de cette communauté. On néglige tout d'abord les dynamiques temporelles (intra et inter annuelles) qui peuvent être importantes à certains endroits. Par exemple, les espèces printanières visitées en plein été auront dans la base de données une abondance sous estimée alors qu'une espèce visitée au moment où elle est la plus abondante verra son abondance surestimée. Les espèces dont l'abondance varie beaucoup au

cours du temps peuvent être considérées comme occupant des niches temporelles distinctes (« storage effect »,Chesson 2000b) et n'auront finalement pas ou peu d'interactions directes. Au contraire, les espèces dont l'abondance varie peu au cours du temps sont susceptibles d'avoir un rôle important dans la structuration des communautés en interagissant directement avec les autres espèces. D'autre part, l'échelle spatiale du relevé ne nous permet pas d'être certain de la proximité des individus des différentes espèces, et donc de l'existence d'interactions biotiques entre certaines espèces. Même si l'on suppose que les espèces abondantes, ayant de nombreux individus dans la communauté, peuvent entrer en compétition avec la majorité des autres espèces, cette hypothèse est probablement fausse pour les espèces peu abondantes (Fig. s.2). Il peut donc y avoir des différenciations de niche spatiales et temporelles à l'intérieur de la communauté considérée (Kneitel & Chase 2004).

(a) **(b)**

Fig. s.2 Deux communautés végétales des Alpes Françaises. (a) Schistes du col du Galibier. Peu d'espèces dominent mais leur abondance est faible. Dans ce genre de milieu, il est peu envisageable que les interactions compétitives soient prédominantes **(b)** Megaphorbiaie au col du Lautaret. Dans ce cas, on peut supposer que les individus de l'espèce dominante (*Adenostyle alliariae*) sont à proximité des individus de toutes les autres espèces, et que cette espèce joue un rôle structurant dans la communauté. Photos : Isabelle Boulangeat, 2008.

DE LA STRUCTURE SPATIALE A LA DISPERSION

Un des résultats majeurs de notre étude sur l'abondance des espèces concerne l'importance de la structure spatiale et de la dispersion (chapitre II). Contrairement aux approches classiques où un terme d'auto-corrélation spatiale est utilisé pour estimer l'effet de la dispersion, nous avons calculé la contribution potentielle de la dispersion à partir d'hypothèses biologiques, à partir de la configuration spatiale des habitats favorables et de la capacité de dispersion des espèces modélisées. Même si notre classification des espèces entre

différents groupes de dispersion peut paraître grossière (chapitre II) notre approche est très conservative car elle permet de séparer des grands groupes d'espèces selon leur capacité supposée de dispersion, sur la base d'un certain nombre de traits biologiques et écologiques (Vittoz & Engler 2007). En effet, l'analyse des patrons d'abondance menée dans le chapitre II montre que des mécanismes source-puits opèrent pour déterminer la distribution des espèces. L'abondance, pour les espèces analysées, est plus forte dans les sites qui sont supposés être des sources que dans ceux qui sont supposés être des puits (Fig. II.5).

Nous avons aussi montré que l'importance relative de la dispersion, par rapport au filtre abiotique et aux interactions biotiques, varie selon les espèces et si l'on s'intéresse à la présence-absence d'une espèce seulement ou à son abondance. Cette différence ne s'explique pourtant pas simplement par la distance de dispersion des graines. En effet, l'importance de l'indice de dispersion qui décrit la proximité de milieux favorables à l'espèce, varie selon les espèces indépendamment de leur capacité de dispersion. Ce résultat suggère que la limitation par la dispersion de l'accès aux sites est vraisemblablement autant le résultat de la configuration spatiale des habitats favorables que de la capacité de dispersion des espèces. En ce qui concerne l'abondance locale des espèces, l'importance ou non de la dispersion peut résulter d'un compromis stratégique. S'il s'agit d'un compromis entre compétition et colonisation, il pourrait être déterminé par une combinaison de traits de dispersion et de traits de compétition. Cette hypothèse reste à explorer.

Dans tous les cas, pour aller plus loin, il faudrait appréhender le mécanisme de dispersion dans son ensemble (parfois appelé migration, Higgins *et al.* 2003), à partir de la production de graines jusqu'à la germination de celles-ci, et déterminer un ensemble de traits qui représenterait l'efficacité de la dispersion. Pour de nombreuses plantes, la majorité des graines tombent dans les 100 m aux alentours (Vittoz *et al.* 2007), et seule une petite poignée qui est dispersée plus loin peut prétendre participer aux effets source-puits et à la colonisation de nouveaux espaces. Le succès de la dispersion dépend fortement de la survie de ces graines et de leur établissement. Au sein même d'une

espèce, si la probabilité de survie des graines était inversement corrélée à leur distance de dispersion, alors les évènements rares de dispersion longue distance seraient plus probables. Pour augmenter le succès d'établissement, les graines peuvent aussi entrer en dormance et attendre plusieurs années que les conditions environnementales soient favorables pour germer. Mieux comprendre la dispersion dans son ensemble permettrait de différencier les espèces selon leurs stratégies et de mieux prédire leurs réponses aux changements environnementaux.

COMMENT TENIR COMPTE DES VARIATIONS TEMPORELLES DE STRUCTURE DES COMMUNAUTES ?

La discussion concernant les interactions biotiques soulève un point très important. Lorsque nous observons les assemblages d'espèces, nous nous plaçons en un point particulier de l'espace et du temps. Selon le moment de l'année, les espèces échantillonnées et leurs abondances relatives peuvent changer dans une même communauté, notamment dus à certains décalages de phénologie. D'une année sur l'autre, les assemblages peuvent également diverger en fonction des d'évènements de dispersion (Kneitel & Chase 2004). Prendre en compte cet aspect temporel lors de l'analyse des données pourrait apporter une meilleure compréhension des mécanismes d'assemblage des communautés.

Une première approche serait l'exploration des variations intra annuelles de la composition et la structure des communautés. Ceci nous permettrait de séparer les espèces qui sont différenciées par des niches temporelles, et entrent peu en interaction, des espèces qui occupent des niches similaires ou totalement chevauchantes et qui sont en interaction directe. Cette approche nécessite de nouvelles données dont nous ne disposons pas à l'heure actuelle, ni dans notre équipe ni en général. Cela demanderait en effet des échantillonnages successifs tout au long de la période de végétation. Le projet TEEMBIO (Towards Eco-Evolutionary Models of BIOdiversity) coordonné par W. Thuiller effectuera de tels relevés dès cet été.

Une deuxième approche possible n'étudierait pas les dynamiques intra-annuelles mais chercherait à mieux exploiter les données existantes.

Pour déterminer le climat associé au relevé, l'idée serait de prendre en compte la date exacte à laquelle le relevé a été fait, et non plus une moyenne sur plusieurs années (ex. Bateman *et al.* 2012). Cette approche permettrait de mieux caractériser la niche climatique des espèces et donc d'établir des prédictions plus robustes, ou de mieux séparer les mécanismes pour les comprendre. La relation ainsi modélisée pourrait être utilisée dans des scenarios où le climat varie chaque année, et serait adaptée pour tester l'effet d'années successives de sècheresses par exemple. En ce qui concerne les interactions biotiques, une idée serait de considérer comme co-occurrentes seules les espèces dominantes dont l'abondance varie peu au cours de l'année (ex. Pellissier *et al.* 2010). Ces espèces sont en effet les plus susceptibles de structurer les interactions biotiques. Leur niche chevauche entièrement celle des autres dans le temps, et leurs individus sont répartis sur toute la surface de la communauté (Fig. s.2b). Les interactions avec les espèces dominantes peuvent être prises en compte dans les modèles statistiques comme une variable environnementale décrivant l'habitat, comme c'est habituellement le cas pour les animaux. La végétation dominante peut également être modélisée dynamiquement, en utilisant un modèle comme celui présenté dans cette thèse (FATE-H). De cette manière, des séquences temporelles de changement de l'habitat pourront être déterminées.

MODÉLISER LA DYNAMIQUE DE LA VÉGÉTATION DOMINANTE

LES LIGNES FORTES DES MECANISMES DE COEXISTENCE RESUMEES DANS DES GROUPES FONCTIONNELS

La modélisation de systèmes complexes tels qu'un écosystème entier nécessite de négliger certains mécanismes et de garder seulement ceux qui sont prépondérants pour prédire la dynamique de ces systèmes. Ici, nous avons commencé par nous focaliser sur la végétation et réduire sa complexité, en représentant des milliers d'espèces végétales par quelques dizaines de groupes fonctionnels végétaux (PFGs), tout en gardant le maximum d'information. Il fallait aussi que les interactions biotiques entre PFGs aient un sens, et que la dynamique des PFGs soit facilement paramétrable. D'un autre côté, les données de traits disponibles pour toutes les espèces sont toujours limitées. Nous avons donc établi une stratégie pour sélectionner un minimum de caractéristiques connues pour la majorité des espèces susceptibles de structurer la végétation. Avec un nombre raisonnable de PFGs (24), il s'agit d'une simplification drastique, mais cette simplification montre des résultats très probants (chapitre III).

La méthode de construction des PFGs que nous avons développée est basée sur le cadre conceptuel présenté dans l'introduction (Fig. i7). Les principaux mécanismes de coexistence qui peuvent déterminer la répartition des PFGs sont pris en compte (i.e. la compétition pour la lumière, la dispersion, et le filtre abiotique régional), ainsi que la réponse des PFGs aux principaux changements environnementaux (climat et pâturage). L'échantillon de traits utilisé pour grouper les espèces dominantes permet aux PFGs d'avoir un comportement homogène lorsqu'ils sont impliqués dans ces processus. Le filtre abiotique est représenté par la niche bioclimatique des espèces, la dispersion est représentée par une classe de distance de dispersion. Les interactions biotiques considérées sont centrées sur la compétition pour la lumière, et deux traits sont utilisés pour la prendre en compte : la hauteur végétative et la préférence lumineuse. La différenciation de

niche est possible par la prise en compte de la démographie, représentée par des types biologiques. En créant 26 groupes à partir de ces traits, nous avons montré que peu d'information est perdue lors de l'estimation de la diversité fonctionnelle (chapitre III). Même si les résultats du modèle dynamique amènent un peu plus d'incertitudes, les patrons de diversité fonctionnelle et de la structure de la végétation actuels sont bien prédits par le modèle (chapitre IV). Ce résultat suggère que les principales stratégies végétales sont correctement décrites par l'ensemble de traits choisis. De plus, leur homogénéité de réponse aux changements de climat (niche climatique similaire) et de pâturage (appétence semblable) permet leur utilisation pour construire des scenarios du futur de la végétation en fonction des changements environnementaux.

Cependant, il ne faut pas perdre de vu le degré de détail représenté, et les limites associées. Par exemple, les résultats du chapitre IV nous suggèrent que les systèmes herbacés sont difficiles à modéliser. Les PFGs de ces milieux, construits à partir de nombreuses espèces, sont tout d'abord assez compliqués à appréhender. D'autre part, le mécanisme de compétition implémenté étant la compétition pour la lumière, sur un pas de temps annuel, il est difficile à paramétrer entre herbacées. Actuellement, la compétition entre herbacées n'est pas modélisée. C'est un problème que la multiplication des groupes d'herbacées ne pourra pas résoudre. De plus, certains traits comme la hauteur végétative des plantes matures varient beaucoup entre populations d'une même espèce, et souvent ne sont pas significativement différents d'une espèce à l'autre (Albert *et al.* 2010a). L'idéal serait de pourvoir prendre en compte ces variations, ainsi que les incertitudes de mesures, lors de la classification, pour construire des groupes fonctionnels plus robustes. Le principal obstacle à cette démarche est de pouvoir estimer une variabilité intra-spécifique pour toutes les espèces de la classification. Ces données seront peut-être disponibles pour beaucoup d'espèces dans les années à venir, mais concernent trop peu d'espèces et de traits aujourd'hui (Kattge *et al.* 2011).

BILAN ET PERSPECTIVES CONCERNANT FATE-H

L'objectif était de développer un modèle dynamique de végétation capable de modéliser la biodiversité (Midgley *et al.* 2010). Nous avons utilisé une approche hybride, assemblant plusieurs sous-modèles pour représenter par des règles, des équations ou des relations statistiques les mécanismes de coexistence principaux (Gallien *et al.* 2010, voir annexe 1). Les filtres abiotiques ont été modélisés par une relation statistique entre la distribution des PFGs et plusieurs variables topo-climatiques. La dispersion a été modélisée comme un processus, considérant les trois phases. La production de graines dépend de l'abondance des plantes matures. Le transfert des graines est stochastique, basé sur la distance de dispersion des graines. L'établissement prend en compte les conditions lumineuses et la qualité de l'habitat. Finalement, le modèle de succession intègre les interactions biotiques à travers la compétition pour la lumière. Le modèle de pâturage permet de tester l'effet de l'utilisation des terres sur la végétation. Les résultats du chapitre IV ont permis de valider le comportement du modèle et son intérêt pour prédire les patrons de biodiversité.

Cependant, la validation du modèle n'est pas évidente. Alors que la répartition actuelle des forêts dans les Alpes et des alpages est en partie le résultat de l'histoire de l'utilisation des terres par l'Homme (Gehrig-Fasel *et al.* 2007; Di Filippo *et al.* 2012), l'état initial de nos modélisations est déterminé par l'état d'équilibre atteint par les PFGs sous les contraintes actuelles d'utilisation des terres et de climat. Il y a donc un écart attendu entre les observations et le résultat des simulations. Dans la limite des connaissances disponibles, nous pourrions inclure certains facteurs historiques dans les modèles d'habitat, pour différencier différentes trajectoires d'utilisation des terres (Quetier *et al.* 2007). De manière générale, la meilleure prise en compte de l'histoire passée de l'utilisation des terres et de l'histoire biogéographique dans les modèles reste un important challenge.

En ce qui concerne le modèle de succession et le modèle de dispersion, inclure plus de détails me paraitrait incohérent par rapport au reste du

modèle. Le premier enjeu serait plutôt de se rapprocher de la relation fondamentale entre climat et PFGs. Ceci va être déterminant pour avoir des scenarios de changement climatique robustes. Une approche pour améliorer cette relation est d'inclure d'autres facteurs explicatifs dans les modèles d'habitat, pour que la relation modélisée avec les facteurs climatiques n'englobe aucun autre phénomène. Quelques pistes ont été proposées dans le chapitre II, mais d'autres sont aussi possibles. Cette approche a aussi ses limites, notamment parce que toutes les combinaisons de facteurs ne sont pas observées, et qu'il n'est donc pas toujours possible de différencier les effets du climat des autres facteurs (Chapitre II). Cependant, un échantillonnage optimisé peut repousser un peu ces limites (Albert *et al.* 2010b; Zurell *et al.* 2012). Un tel échantillonnage se dessine dans l'espace des variables explicatives, et l'objectif est de quadriller cet espace. Les points ainsi choisis sont une combinaison des facteurs explicatifs et s'ils existent à plusieurs endroits géographiques, sont déterminés au hasard, ou bien au plus pratique.

En ce qui concerne le modèle de perturbation (pâturage et fauche), il est difficile à paramétrer, et les avis d'experts concernant les valeurs fourragères et la palatabilité des espèces sont parfois divergents. Cependant, l'effet général du pâturage dans le modèle FATE-H est cohérent avec les observations (chapitre IV). L'amélioration dont l'enjeu semble le plus grand serait de pouvoir modéliser l'effet du moment de l'année où a lieu le pâturage. En effet, les agriculteurs modifient cette date chaque année selon le climat, et les effets sur la végétation pourraient être grands étant donné que certaines espèces ne pourraient pas fructifier si les troupeaux arrivaient trop tôt.

Pour pallier au manque de mécanismes de coexistence chez les herbacées, le plus simple serait peut-être d'introduire un paramètre décrivant la phénologie des espèces. Ainsi, les strates de hauteurs au dessous d'un mètre pourraient être détaillées et la compétition pour la lumière pourrait avoir lieu entre herbacées qui utilisent les mêmes fenêtres phénologiques. Dans un deuxième temps, ce paramètre de phénologie pourrait varier en fonction du climat. Ceci est très

intéressant puisque les décalages phénologiques sont une réponse directe au changement climatique déjà observé (Hughes 2000).

VERS UNE MODÉLISATION MULTI-TROPHIQUE DE L'ÉCOSYSTÈME

Les perspectives de développement et d'utilisation de FATE-H visent l'inclusion d'autres niveaux trophiques (Midgley *et al.* 2010 McRae *et al.* 2008 et Fig. s.3). Par exemple, le modèle dynamique de la végétation peut être combiné avec un modèle de métapopulations (ex. Keith *et al.* 2008) ou tout autre modèle de dynamique de populations (Gallien *et al.* 2010, annexe 1). Le principal challenge reste l'articulation entre les sous-modèles. Plusieurs modèles démographiques prennent déjà en compte l'influence de l'habitat sur la démographie de l'espèce cible, mais la rétroaction de la dynamique des populations animales sur la végétation reste un défi majeur. Dans FATE-H, une voie d'entrée est le modèle de perturbation, qui peut, à partir de la distribution spatiale des espèces animales à chaque pas de temps, et de règles d'interactions, influencer la dynamique des PFGs. Il serait intéressant mais plus difficile d'agir sur la dispersion des plantes, tout en gardant un temps raisonnable de simulation à l'échelle régionale.

Comme la répartition de nombreux animaux est directement influencée par la végétation, le couplage de FATE-H à un modèle démographique concernant une espèce cible ouvrirait de nombreuses possibilités (Fig. s.3). La gestion des espèces dont la démographie est contrôlée, comme les grands herbivores ou les espèces invasives, ou au contraire des espèces menacées comme le chardon bleu (*Eryngium alpinum*) ou certaines chauves-souris, pourraient bénéficier d'un tel développement.

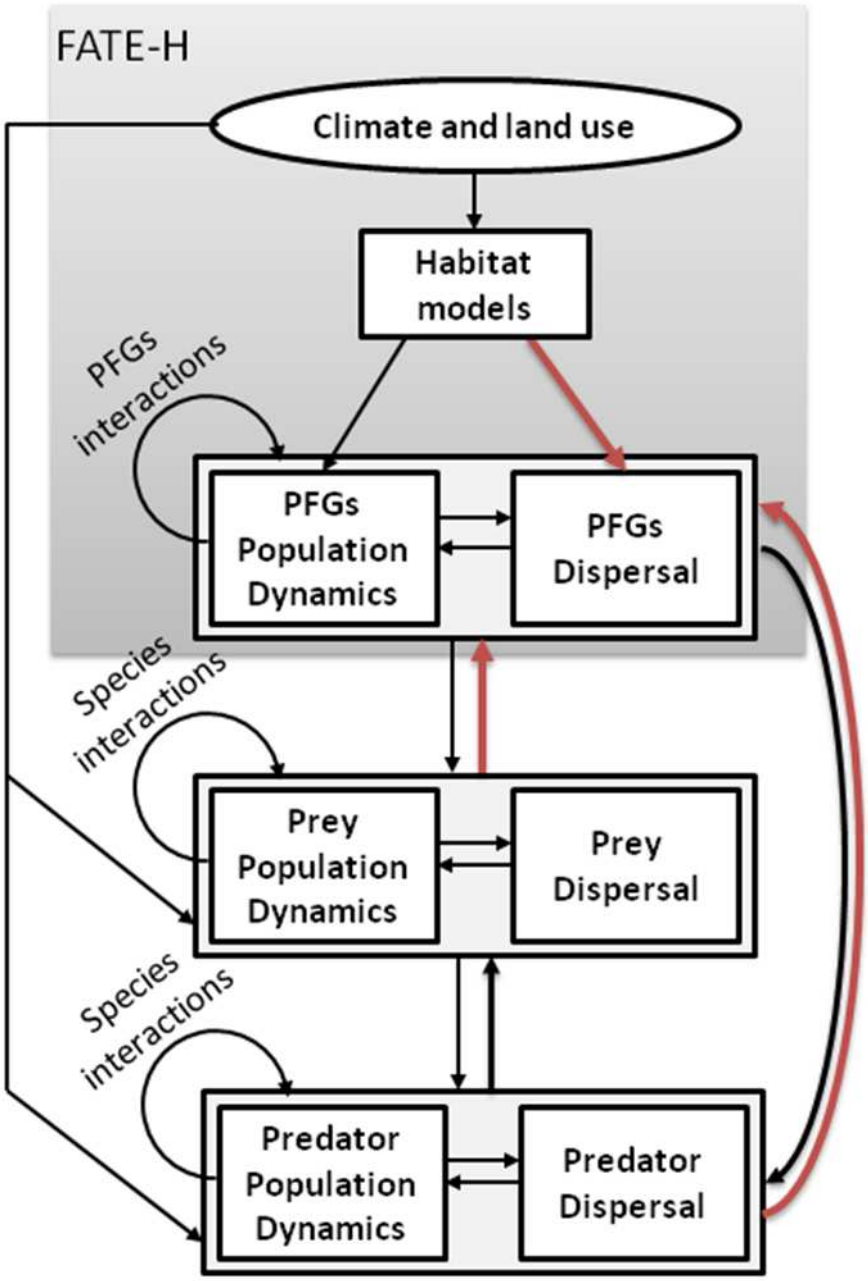


Fig. s.3 Structure générale d'un modèle plus complet de l'écosystème. La zone grisée correspond à ce qui est couvert par le modèle FATE-H. La partie de couplage avec un modèle animal, ou un système prédateur-proie reste à développer. De nombreuses rétroactions peuvent être considérées, notamment celles des animaux sur la dynamique de la végétation.

QUELLES IMPLICATIONS POUR LA CONSERVATION ?

DU POINT DE VUE DES ESPÈCES

La spécialisation des plantes est un aspect très important en biologie de la conservation. Les espèces spécialistes peuvent en effet répondre de manière plus forte aux perturbations qui modifient leurs habitats que les généralistes, et seront dans ce cas plus propices à l'extinction (Evans *et al.* 2005; Willson *et al.* 2008). Ceci a été montré pour de nombreux taxa (ex. oiseaux, Jiguet *et al.* 2007 ; plantes, Thuiller *et al.* 2004a). Si ces espèces sont également très localisées, dans des habitats menacés, et contiennent peu d'individus dans chaque population, leur vulnérabilité est maximale. Les analyses du chapitre I montrent que ces caractéristiques ne sont pas toujours associées (Fig. I.4). Une grande partie des espèces les plus spécialistes étudiées sont localement abondantes comparée aux autres espèces (ex. *Juncus subnodulosus*). D'un autre côté, les espèces les plus spécialistes ont, en général, une répartition géographique très restreinte, ce qui fait qu'elles sont souvent la cible des mesures de protection (ex. *Scheuchzeria palustris*, *Genista delphinensis*, *Carex maritima*, *Drosera rotundifolia*). A l'inverse, les espèces endémiques ne sont pas toutes spécialistes d'habitat (ex. *Delphinium dubium*), et dans ce cas, devraient être moins sensibles aux changements environnementaux. C'est aussi le cas des annuelles (Marini *et al.* 2012), dont l'environnement biotique peut être varié, et qui devraient être plus tolérantes aux changements de leur environnement, tant qu'il n'est pas détruit. Enfin, l'extinction des espèces vulnérables (i.e. endémiques et spécialiste occupant des habitats menacés), entrainerait une diminution de la diversité spécifique, mais pourrait avoir un impact plus diffus sur d'autres facettes de la diversité comme la diversité phylogénétique (Thuiller *et al.* 2011, voir annexe 3).

DU POINT DE VUE DES HABITATS

Dans le Chapitre II, nous avons vu que les zones humides, les plaines alluviales, les landes et les forêts de chêne à feuilles persistantes abritent de nombreuses espèces spécialistes (Fig. I.3). D'autres occupent les espaces d'altitude comme les pelouses alpines et les falaises. Cependant, tous ces habitats ne sont pas menacés de la même manière par les changements environnementaux. Par exemple, les falaises subissent peu l'impact anthropique, contrairement aux plaines alluviales. Si l'on considère la complexité des habitats, elle est plus importante en forêt (Chapitre IV) alors que les espèces endémiques de plantes se trouvent principalement dans les pelouses d'altitude et les rochers (Fig. s.4).

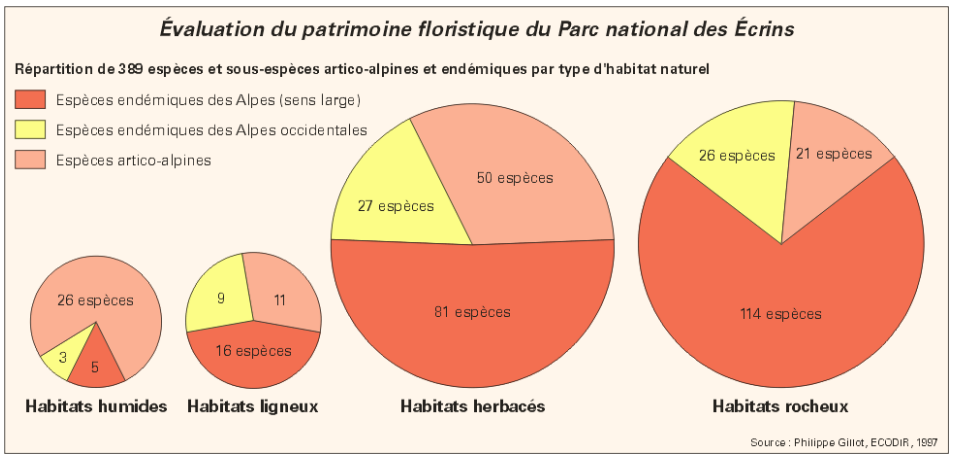


Fig. s.4 La répartition des espèces endémiques du Parc des Ecrins dans quatre habitats.

Ces contradictions nous montrent que la protection de quelques espèces rares ne peut pas résoudre la crise de la biodiversité dans son ensemble. De manière générale, l'approche traditionnelle de conservation de la biodiversité, qui met la priorité sur des espèces endémiques, spécialistes ou patrimoniales, sans considérer les écosystèmes dans leur ensemble, est remise en cause. Cela nous pousse à considérer les multiples échelles spatiales et temporelles qui concernent la genèse de la biodiversité et son déclin. Par exemple, les habitats abritant les spécialistes sont non-seulement importants à préserver pour les espèces qu'ils contiennent mais aussi car ils font partie des facteurs à l'origine des processus de spécialisation. Comprendre les mécanismes de maintenance de la biodiversité et préserver les conditions environnementales permettant leur fonctionnement est probablement l'enjeu majeur de la biologie de la conservation au XXIème siècle.

EXPLORER DES SCENARIOS POSSIBLES DE LA VÉGÉTATION DANS LES ÉCRINS

Le chapitre V nous a permis de mettre en évidence l'intérêt d'un modèle dynamique de la végétation pour comprendre et prédire les éventuels changements de paysage en réponse aux changements environnementaux. L'importance de la dynamique temporelle est mise en évidence par le temps de réponse de la végétation au changement climatique. Pendant les 100 premières années, où le changement est effectif, la structure du paysage (mesuré par le pourcentage de milieux fermés) reste la même à tous les étages de végétation. Ce n'est qu'après ce délai que la fermeture des milieux apparait (chapitre V). Ces résultats insistent sur l'importance de considérer les potentiels décalages temporels entre le changement environnemental et son effet, et s'ajoutent à quelques autres études qui suggèrent que l'impact du climat et la colonisation des nouveaux espaces favorables par la forêt sont décalés dans le temps (ex. Rupp *et al.* 2001; Dullinger *et al.* 2012). Au contraire, la réponse à une modification du pâturage est beaucoup plus rapide. L'intensification du pâturage rouvre le milieu et les zones abandonnées sont très vite recolonisées par la forêt. Cette rapide réponse peut s'expliquer par le fait que les forêts ne sont probablement pas loin des pâturages abandonnés et le climat est déjà favorable dans ces zones les plus proches (Fig. s.5).

Fig. s.5 Recolonisation des pâturages récemment abandonnés par l'Aulne vert (*Alnus viridis*) et le mélèze (*Larix decidua*). Col du Lautaret, 2000m. Photo : Isabelle Boulangeat, 2008.

Un deuxième résultat très important du chapitre V est l'interaction entre les effets du changement climatique et ceux de l'abandon du pâturage. En effet, lorsque les deux scenarios sont combinés, la colonisation des pâturages abandonnés dans un premier temps, permet aux arbres de s'implanter très rapidement dans les zones rendues favorables par le changement climatique. Cette synergie a pour effet final de réduire la diversité beta des PFGs, alors qu'elle se maintenait dans chacun des scenarios séparément.

Ces résultats démontrent l'intérêt des développements réalisés au cours de cette thèse, qui ouvrent la voie à l'étude de scenarios plus complexes, mettant en jeu des évènements extrêmes (ex. sècheresse successive), modifiant leur fréquence et leur intensité. Ce modèle permettra d'explorer les effets spatiaux et temporels de la dynamique des populations dans un environnement hétérogène et fluctuant dans le temps.

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ANNEXES

Les annexes ont pour but de présenter les travaux secondaires dans lesquels j'ai participé pendant ma thèse. Chaque article y est représenté par son abstract.

Annexe 1. Gallien, L., Münkemüller, T., Albert, C.H., **Boulangeat, I.** & Thuiller, W. (2010) Predicting species invasions: where to go from here? *Diversity and Distributions*, **16**, 331-342.

Annexe 2. Thuiller W., Gallien, L., **Boulangeat, I.,** de Bello, F., Münkemüller, T., Roquet-Ruiz, C. & Lavergne, S. (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions*, **16**, 461-475.

Annexe 3. Thuiller, W., Lavergne, S., Roquet, C., **Boulangeat, I.**, Lafourcade, B. & Araújo, M.B. (2011) Consequences of climate change on the Tree of Life in Europe. *Nature*, **470**, 531-534

Annexe 4. Albert, C.H., de Bello, F., **Boulangeat, I.,** Pellet, G., Lavorel, S. & Thuiller, W. (2012) On the importance of intraspecific variability for the quantification of functional diversity. *Oikos*, **121**, 116-126.

Annexe 5. de Bello, F., Lavorel, S., Lavergne, S., Albert, C.H., **Boulangeat, I.,** Mazel, F. & Thuiller, W. (2012) Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography.* In press.

Annexe 6. Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., **Boulangeat, I.,** Hodgson, J.A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V.M., Bullock, J.M. Dispersal and biodiversity responses to climate change. *Submitted.*

Annexe 7. Meynard, C.H., Lavergne, S., **Boulangeat, I.,** Garraud, L., Van Es, J., Mouquet, N., Thuiller, W. Disentangling the drivers of metacommunity structure across spatial scales. *Submitted*.

Gallien, L., Münkemüller, T., Albert, C.H., **Boulangeat, I.** & Thuiller, W. (2010) Predicting species invasions: where to go from here? *Diversity and Distributions*, **16**, 331-342.

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BIODIVERSITY REVIEW

Predicting potential distributions of invasive species: where to go from here?

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ABSTRACT

Aim There has been considerable recent interest in modelling the potential distributions of invasive species. However, research has developed in two opposite directions: the first, focusing on screening, utilizes phenomenological models; the second, focusing on predictions of invasion dynamics, utilizes mechanistic models. Here, we present hybrid modelling as an approach to bridge the gap and to integrate the advantages of both research directions.

Location Global.

Methods First, we briefly summarize the characteristics and limitations of both approaches (screening vs. understanding). Then, we review the recent developments of hybrid models, discuss their current problems and offer suggestions to improve them.

Results Generally, hybrid models are able to combine the advantages of currently used phenomenological and mechanistic approaches. Main challenges in building hybrid models are the choices of the appropriate degree of detail and efficiency and the decision on how to connect the different sub-models. Given these challenges, we discuss the links between the phenomenological and the mechanistic model parameters, the underlying concepts of fundamental and realized niches and the problem of feedback loops between population dynamics and environmental factors.

Main conclusions Once the above challenges have been addressed and the necessary framework has been developed, hybrid models will provide outstanding tools for overcoming past limitations and will provide the means to make reliable and robust predictions of the potential distribution of invasive species, their population dynamics and the potential outcomes of the overall invasion process.

Keywords

Biological invasions, habitat suitability model, hybrid model, invasion dynamics, mechanistic model, species distribution model.

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Thuiller W., Gallien, L., **Boulangeat, I.,** de Bello, F., Münkemüller, T., Roquet-Ruiz, C. & Lavergne, S. (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions*, **16**, 461-475

Diversity and Distributions, (Diversity Distrib.) (2010) 1–15

BIODIVERSITY REVIEW

Resolving Darwin's naturalization conundrum: a quest for evidence

Wilfried Thuiller*†, Laure Gallien, Isabelle Boulangeat, Francesco de Bello‡, Tamara Münkemüller, Cristina Roquet and Sébastien Lavergne†

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ABSTRACT

Aim The study of biological invasions has long considered species invasiveness and community invasibility as separate questions. Only recently, there is an increasing recognition that integrating these two questions offers new insights into the mechanisms of biological invasions. This recognition has renewed the interest in two long-standing and seemingly contradictory hypotheses proposed by Darwin: phylogenetic relatedness of invaders to native communities is predicted to promote naturalization because of appropriate niche-adaptation but is at the same time predicted to hamper naturalization because of niche overlap with native species. The latter is known as Darwin's naturalization hypothesis.

Location Global.

Methods and Results We review the studies that have tested these hypotheses and summarize their largely inconsistent outcomes. We argue that most of the inconsistency arises from discrepancies in the applied conceptual frameworks and analytical approaches and not from different model organisms and different ecological contexts. First, observed patterns and results can be seriously flawed by different spatial and phylogenetic scales, which do not equally reveal community assembly mechanisms. Second, different studies have used different metrics, which may test for different specific hypotheses. Thus, we propose a set of metrics derived from the alpha niche concept to measure invaders relatedness to native communities. Finally, approximating species niche differentiation from phylogenetic relatedness is not exempt of assumptions, and invasive species naturalization may result from various ecological mechanisms of biotic resistance that are not necessarily revealed by species phylogeny alone.

Main conclusions The quest for resolving the conundrum of Darwin's naturalization hypothesis will only be successful if appropriate scales, metrics and analytical tests are thoroughly considered. We give several recommendations and suggest, whenever possible, to use trait-based measurements of species dissimilarity as the most promising avenue to unravel the mechanisms driving alien species invasions.

Keywords
Alpha niche, biological invasions, community invasibility, community phylogenetics, ecological niche, environmental filtering, niche differentiation, null models, phylogenetic relatedness.

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Thuiller, W., Lavergne, S., Roquet, C., **Boulangeat, I.**, Lafourcade, B. & Araújo, M.B. (2011) Consequences of climate change on the Tree of Life in Europe. *Nature*, **470**, 531-534

LETTER

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Consequences of climate change on the tree of life in Europe

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Many species are projected to become vulnerable to twenty-first-century climate changes[1,2], with consequent effects on the tree of life. If losses were not randomly distributed across the tree of life, climate change could lead to a disproportionate loss of evolutionary history[3–5]. Here we estimate the consequences of climate change on the phylogenetic diversities of plant, bird and mammal assemblages across Europe. Using a consensus across ensembles of forecasts for 2020, 2050 and 2080 and high-resolution phylogenetic trees, we show that species vulnerability to climate change clusters weakly across phylogenies. Such phylogenetic signal in species vulnerabilities does not lead to higher loss of evolutionary history than expected with a model of random extinctions. This is because vulnerable species have neither fewer nor closer relatives than the remaining clades. Reductions in phylogenetic diversity will be greater in southern Europe, and gains are expected in regions of high latitude or altitude. However, losses will not be offset by gains and the tree of life faces a trend towards homogenization across the continent.

Albert, C.H., de Bello, F., **Boulangeat, I.,** Pellet, G., Lavorel, S. & Thuiller, W. (2012) On the importance of intraspecific variability for the quantification of functional diversity. *Oikos*, **121**, 116-126.

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On the importance of intraspecific variability for the quantification of functional diversity

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Functional diversity (FD) is a key facet of biodiversity used to address central questions in ecology. Despite recent methodological advances, FD remains a complex concept and no consensus has been reached either on how to quantify it, or on how it influences ecological processes. Here we define FD as the distribution of trait values within a community. When and how to account for intraspecific trait variability (ITV) when measuring FD remains one of the main current debates. It remains however unclear to what extent accounting for population-level ITV would modify FD quantification and associated conclusions. In this paper, we address two critical questions: (1) How sensitive are different components of FD to the inclusion of population-level ITV? (2) Does the omission of ITV obscure the understanding of ecological patterns? Using a mixture of empirical data and simulation experiments, we conducted a sensitivity analysis of four commonly used FD indices (community weighted mean traits, functional richness, Rao's quadratic entropy, Petchey and Gaston's FD index) and their relationships with environmental gradients and species richness, by varying both the extent (plasticity or not) and the structure (contingency to environmental gradient due to local adaptation) of population-level ITV. Our results suggest that ITV may strongly alter the quantification of FD and the detection of ecological patterns. Our analysis highlights that 1) species trait values distributions within communities are crucial to the sensitivity to ITV, 2) ITV structure plays a major role in this sensitivity and 3) different indices are not evenly sensitive to ITV, the single-trait FD from Petchey and Gaston being the most sensitive among the four metrics tested. We conclude that the effects of intraspecific variability in trait values should be more systematically tested before drawing central conclusions on FD, and suggest the use of simulation studies for such sensitivity analyses.

de Bello, F., Lavorel, S., Lavergne, S., Albert, C.H., **Boulangeat, I.,** Mazel, F. & Thuiller, W. (2012) Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps, *Ecography,* In press.

Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps

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Abstract

Understanding the influence of the environment on the functional structure of ecological communities is essential to predict the response of biodiversity to global change drivers. Ecological theory suggests that multiple environmental factors shape local species assemblages by progressively filtering species from the regional species pool to local communities. These successive filters should influence the various components of community functional structure in different ways. In this paper, we tested the relative influence of multiple environmental filters on various metrics of plant functional trait structure (i.e. 'community weighted mean trait' and components of functional trait diversity, i.e. functional richness, evenness and divergence) in 82 vegetation plots in the Guisane Valley, French Alps. For the 211 sampled species we measured traits known to capture key aspects of ecological strategies amongst vascular plant species, i.e. leaf traits, plant height and seed mass (LHS). A comprehensive information theory framework, together with null model based resampling techniques, was used to test the various environmental effects. Particular community components of functional structure responded differently to various environmental gradients, especially concerning the spatial scale at which the environmental factors seem to operate. Environmental factors acting at a large spatial scale (e.g. temperature) were found to predominantly shape community weighted mean trait values, while fine-scale factors (topography and soil characteristics) mostly influenced functional diversity and the distribution of trait values among the dominant species. Our results emphasize the hierarchical nature of ecological forces shaping local species assemblage: large-scale environmental filters having a primary effect, i.e. selecting the pool of species adapted to a site, and then filters at finer scales determining species abundances and local species coexistence. This suggests that different components of functional community structure will respond differently to environmental change, so that predicting plant community responses will require a hierarchical multi-facet approach.

Keywords: assembly rules, species coexistence, community mean trait values, LHS, inference model, plant diversity

Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., **Boulangeat, I.,** Hodgson, J.A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V.M., Bullock, J.M. Dispersal and biodiversity responses to climate change. *Submitted.*

Dispersal is fundamental in determining biodiversity responses to rapid climate change, but recently acquired ecological and evolutionary knowledge is yet to be incorporated into either predictive methods or conservation management. Accumulating evidence demonstrates direct impacts of climate change on dispersal. Additionally, evolutionary theory predicts increases in dispersal at expanding range margins, and this has been observed in a number of species. This multitude of ecological and evolutionary processes is likely to lead to complex responses of dispersal to climate change. As a result, improvement of models of species' range changes will require greater realism in the representation of dispersal. Placing dispersal at the heart of our thinking will facilitate development of climate-proof conservation strategies, including landscape management and assisted colonisation.

Meynard, C.H., Lavergne, S., **Boulangeat, I.,** Garraud, L., Van Es, J., Mouquet, N., Thuiller, W. Disentangling the drivers of metacommunity structure across spatial scales. *Submitted*.

Abstract

Different metacommunity theories attribute different importance to dispersal, environmental filtering, biotic interactions and stochastic events in community assembly. How spatial scale determines their relative effects is still unclear. We used two approaches across five different spatial resolutions (1-km to 30-km) to disentangle these effects: variance partitioning on species diversity and analysis of species co-occurrence patterns across environmental gradients. Both strategies provide consistent and complementary results. We reveal a strong influence of environmental filtering across resolutions, with a greater explained variance on species richness when aggregating the data at coarser spatial resolutions. Dispersal limitation, although not the primary structuring force in these communities, has noticeable effects at all resolutions and is difficult to separate from the spatially correlated environmental effects. Co-occurrence analysis shows that communities are changing synchronously along environmental gradients at all spatial resolutions. While co-occurrence patterns allow for a more direct link between empirical patterns and ecological theory, variance partitioning allows showing the potential role of dispersal across scales, even if this is not the dominant process. Both approaches have their limitations and advantages. We argue that by using a combination of methods rather than a single approach we get a more robust understanding of forces structuring ecological communities.

Keywords

Community assembly, co-occurrence, metacommunities, plant communities, variance partitioning.

Résumé

Les conséquences des récents changements environnementaux sont déjà observables sur les écosystèmes du monde entier et menacent la biodiversité. Dans l'objectif de conserver les bénéfices que nous procurent les écosystèmes, l'enjeu est de comprendre et prédire la dynamique spatiale et temporelle des paysages et de la biodiversité afin de mieux anticiper les changements possibles et adapter les décisions de conservation. En zone de montagne, où l'environnement est très hétérogène, les effets combinés des modifications du climat et de l'agriculture sont susceptibles d'avoir un impact important sur les écosystèmes. La présente thèse a pour objectif principal de caractériser les espèces et les habitats vulnérables aux changements climatiques et changements d'utilisation des terres dans les Alpes Françaises. Elle apporte sa contribution en se basant sur des données accumulées par le Conservatoire Botanique National Alpin et le Parc national des Ecrins (PNE), et en utilisant trois angles d'approche complémentaires. Dans une première partie, les cadres théoriques expliquant la coexistence des espèces et leur répartition spatiale ont été testés empiriquement. Les patrons de rareté des plantes des Alpes françaises ont ainsi été reliés aux caractéristiques des espèces, mettant en évidence les compromis entre différentes stratégies fonctionnelles. Une seconde analyse de la répartition de 21 espèces cibles a démontré la différence entre les facteurs expliquant la présence d'une espèce à un endroit donné et ceux expliquant son abondance. Cette analyse a également permis de souligner l'importance de la dispersion et mis en évidence des dynamiques source-puits chez certaines espèces. La deuxième partie s'appuie sur les mêmes cadres théoriques et a consisté à développer un modèle dynamique de la structure et de la diversité de la végétation. Ce modèle a été calibré et validé sur la végétation du PNE. Une troisième partie porte son attention sur les évolutions possibles de la végétation sous plusieurs scénarios de changements climatiques et d'utilisation des terres. Les simulations ont montré qu'il est nécessaire de considérer la dynamique temporelle du fait que les conséquences d'un changement climatique peuvent être observées bien après la phase du changement. D'autre part, l'analyse a montré les effets conjugués que peuvent avoir les changements climatiques et la déprise agricole sur la structure de la végétation. Un tel modèle ouvre la voie à l'exploration de multiples scenarios, en permettant non seulement de décrire des paysages futurs potentiels mais aussi les états de transition qui devraient y mener.

Summary

On-going global changes have already affected ecosystems and threaten the biodiversity all over the world. In order to maintain the ecosystems services provided to humans and adapt conservation planning, the challenge is to improve our understanding of the mechanisms underlying the maintenance of biodiversity and to predict its response to global changes. In mountainous areas, where the environment is very heterogeneous, the modifications of both climate and land use are expected to strongly influence the landscapes and current biodiversity. This PhD thesis has for main objective to assess the vulnerability of species and habitat to environmental changes in the French Alps. It uses three different approaches and relies on the large databases accumulated by two institutions: the National Alpine Botanical Conservatory and the Ecrins National Park (PNE). The first part of the PhD confronts theoretical hypotheses for species coexistence to observations and describes the characteristics of the regional flora. The species ecological niche breadth has been estimated and related to other rarity facets and trade-off between plant functional strategies. A second analysis disentangles the drivers of the presence or the local abundance of 21 focal species and highlights the importance of the dispersion and the source-sink dynamics. The second part is based on the same conceptual background and aims to develop a dynamic model of the vegetation structure and diversity. The model has been validated for the vegetation of the PNE. The last part proposes an application of this dynamic model to provide multiple biodiversity scenarios in respect to change in both climate and land management. The simulations showed that the consequences of climate change might be visible only after a certain time-lag, demonstrating the interest of considering the spatial but also temporal vegetation dynamics. Furthermore, the analysis pointed out the importance of the interplay effects between climate and land use abandonment. Such a model should pave the way for the exploration of multiples scenarios and will be able to describe not only the potential future landscapes but also the transition states leading to it.